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RPHOLOGY OF THE DIENCEPHALIC FLOOR

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The Morphology of the Diencephalic Floor

A Contribution to the Study of Craniate Homology

FREDERICK TILNEY

From the Department of Anatomy, Columbia University

Reprinted from THE JOURNAL OF COMPARATIVE NEUROLOGY,
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THE MORPHOLOGY OF THE DIENCEPHALIC FLOOR

A CONTRIBUTION TO THE STUDY OF CRANIATE HOMOLOGY

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THIRTY FIGURES

The fact that the basal surface of the brain-stem is phyletically more constant in form than the lateral walls or the roof is so obvious as scarcely to need mention; yet in some respects it is a fact of considerable significance. It seems to have importance in estimating the homological values of certain parts of the basal region since this region in consequence of its greater morphological constancy should afford more exact evidence of homology. This becomes especially clear when it is considered how plastic are the lateral walls of the neural tube, not only in their embryonic development but in the adaptive modifications of which they are capable. A similar plasticity is seen in the roof-plate as witnessed by the varied conformation of the paraphysis, habenular region, epiphysis, mesencephalic tectum and cerebellum.

The basal region, on the other hand, is not without its variations; nor is it surprising that this region should bear traces of primitive characters, particularly in the interbrain, where the neural structures have always maintained such intimate relations to the stomadaeum, pituitary gland and branchial cavity. Andriezen (1), among others, has brought this fact out clearly. He observed in Ammocoetes, Amphioxus and Balanoglossus, as well as in the larval and adult forms of Ascidians, a small tubular aqueduct of capillary lumen and lined by ciliated epithelium, extending between the mouth cavity and the forebrain. This bucco-neural duct, he believes, provides a true water-vascular system for the central nervous

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tissue. To the collection of ganglionic cells situated at the upper end of this duct he attributes a function similar to that of the osphradial organ in mollusca, thus bringing it into general relation with the olfactory apparatus. . It is also his opinion that the hypophysis, in this sense, was functionally active in the ancestral vertebrates and that while the bucco-neural duct has been obliterated the sub-neural or pituitary gland with the collection of ganglionic cells has persisted. Ayers (2) is in accord with this theory when he states that the hypophysis arose as an organ of taste and the infundibulum was its nerve. Further evidence of this kind is furnished by Ganin (3), who was among the first to observe a connection between the anterior extremity of the embryonic neural tube and the branchial cavity in Ascidians. Similar observations were made upon chordata by Kowalevsky (4), Ussow (5), Julin (6) and von Kuppfer (7); the latter expressing himself as follows: "Der Verbindungskanal zwischen Hirn und Darm schlage ich vor als Canalis Neurentericus anterior zu bezeichen und die Glande hypophysaire von van Beneden und Julin wäre wohl am einfachsten als Neural-drüse zu benennen."

It seems probable in the light of these observations that such variations as do appear in the floor of the interbrain of craniates are adaptive in their nature. This idea is borne out by the fact that of all the structures arising from the diencephalic floor-plate the infundibular process is the most variable. This process from its early phases of development in all forms maintains close relation to the stomadaeum, pituitary evagination and branchial cavity. As an adult structure its modifications are numerous.

In the selachian (Mustelus laevis; fig. 1, A) the processus infundibuli projects caudad from the floor of the third ventricle; it presents two surfaces, i.e., a *ventral* or *pituitary surface* in contact with the pituitary gland, and a *dorsal* or *saccular surface* which is much convoluted and highly vascular forming the *saccus vasculosus*. In the amphibian (Rana pipiens; fig. 1, B) the same general relations obtain and the two characteristic surfaces are present except that the dorsal or saccular surface

is less convoluted and less vascular, while the ventral one has increased in thickness.

In sauropsids, for birds as well as reptiles, the infundibular process differs in certain details from that of the ichthyopsid although the general homology of the structure in all these forms is discernible. In all three instances the cavity of the third ventricle extends into the infundibular process. In the selachian and amphibian this communication is not defined by any marked constriction. The bird (Gallus gallus; fig. 1, C) on the other hand, shows a distinct constriction in the region where the cavity of the general ventricular chamber passes over into the recess of the infundibular process. The process still presents its two characteristic surfaces: the pituitary surface is in contact with the pituitary gland, while the dorsal or saccular surface is much convoluted and non-vascular. This surface, unlike that in the frog and dog-fish, is thick. The recess of the infundibular process in the bird as in the other forms already described presents numerous branching diverticula.

The mammalian structure is characterized by a marked change in that the cavity of the third ventricle does not extend into the infundibular process which latter, in consequence, becomes solid except for a small proximal portion of its stem. These conditions are shown in the dog (fig. 1, E). So far as I am able to state at present one family alone, the Felidae, departs from the mammalian type in this respect. Here the third ventricle actually communicates with a large recess in the infundibular process by means of a narrow, tubular canal which passes from the ventricle through the stem of the process (fig. 1, D). The recess of the infundibular process shows no branching diverticula; the walls which bound it are thick and non-vascular, so that from all appearances it may be inferred that the convoluted saccular surface, so conspicuous in the selachian, amphibian and sauropsid, has been replaced by a now very extensive pituitary surface. This supposition is rendered more probable by the fact that the entire infundibular process in the mammal is completely invested by the tissue of the pituitary gland. In the anthropoids and man (fig. 1, F) the solidification

ANNOTATIONS FOR ALL FIGURES

1, Aqueduct of Sylvius
2, Chiasmatic process
3, Cerebellum
4, Chiasm
5, Corpus interpedunculare
6, Diverticula sacci vasculosi
7, Epiphysis
8, Ectoptic zone of Schulte
9, Foramen of Monro
10, Hypophyseal recess
11, Infundibular stem
12, Infundibular canal
13, Infundibular process
14, Infundibular process; saccular surface (saccus vasculosus)
15, Infundibular process; pituitary surface
16, Infundibular process, lateral process
17, Infundibular region
18, Infundibular evagination
19, Interoptic groove
20, Lamina terminalis
21, Lateral process of post-chiasmatic eminence (lobus inferior)
22, Lateral eminence
23, Median post-chiasmatic groove
24, Mid-brain
25, Mammillary region
26, Mammillary recess
27, Mammillary body (posterior lobe)
28, Neuropore
29, Optic vesicle or evagination
30, Optic peduncle
31, Optico-infundibular groove
32, Post-chiasmatic eminence (lobus inferior)
33, Post-chiasmatic recess (recess of inferior lobe)
34, Post-infundibular eminence
35, Post-infundibular recess
36, Post-infundibular evagination
37, Post-mammillary evagination
38, Prechiasmatic recess
39, Paraphysis
40, Recess of infundibular process or of infundibular evagination
41, Supraoptic crest
42, Supraoptic recess
43, Thalamencephalon
44, Telencephalon
45, Tuberculum postero-superius
46, Tubercle of the floor of Schulte
47, Velum transversum

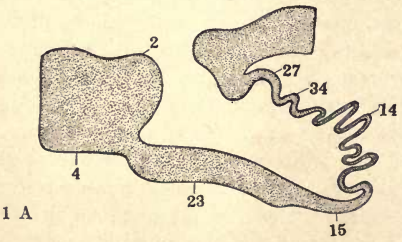
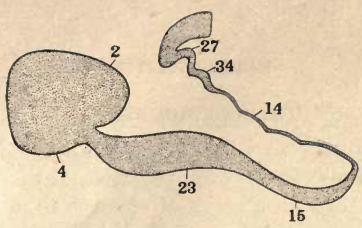


Fig. 1 Comparative series of infundibular region. A, dog-fish; B, frog; C, fowl; D, cat; E, dog; F, man. *2*, chiasmatic process; *4*, chiasm; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *23*, median post-chiasmatic groove; *27*, mammillary body (posterior lobe); *34*, post-infundibular eminence.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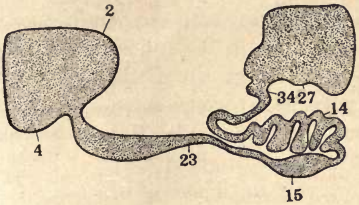
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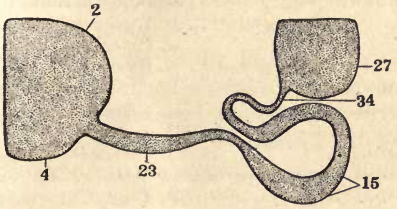
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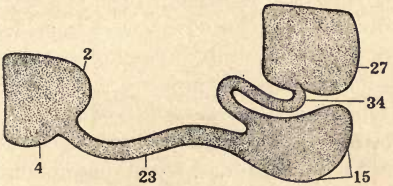
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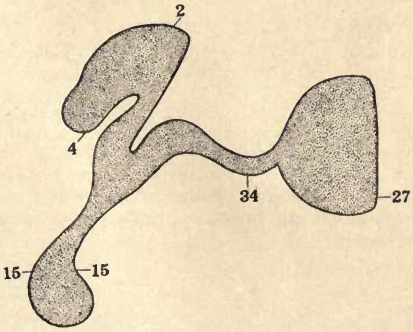
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1 F

of the infundibular process and the exclusion from it of any accessory recess of third ventricle have progressed to the most extreme degree, for in these forms even the stem of the process is solid.

In this way through a series of changes from the ichthyopsid to the mammal the evolution of the infundibular process may be traced. In this series the sauropsid condition still bears evidence of the saccus-formation in its apparently retrograding saccular surface; the conditions in the Felidae carry this retrograding process one step further toward the general mammalian type of infundibular process from which the saccular surface and the saccus-formation have entirely disappeared.

It is not, however, until the entire floor of the ventricle is considered that the significance of each of its several parts may be ultimately determined. These parts have been designated by many terms, several of which have been devised with the intention of giving a phylogenetic or embryological interpretation to the structures. Such, for example, is the case with the part described by Retzius (9) as the *eminentia saccularis*, for this term as applied to mammals imputes a genetic relationship between the eminence so described and the *saccus vasculosus* of fish. That such a relationship does not actually exist can, I think, be proved. For these reasons in considering this region of the brain it seems advisable to employ such terms only as shall be morphologically or topographically descriptive. To this end the following suggestions are offered for the structures found upon the floor of the third ventricle, beginning at the optic chiasm and proceeding caudad to the mammillary bodies:

1. The *optic chiasm.*

2. The *supraoptic crest,* a transverse ridge extending across the dorso-cephalic surface of the optic chiasm and for a short distance upon the optic nerves.

3. The *post-chiasmatic eminence,* a marked protuberance of the floor immediately caudad to the chiasm; this structure is often referred to as the *bulbus infundibuli.*

4. The *infundibular process,* an expanded appendage to the floor connected with the infundibular bulb by the *infundibular stem.*

5. The *post-infundibular eminence*, a small irregular and median protuberance in front of the corpora mammillaria and caudad to the infundibular bulb.

6. The *mammillary bodies*.

7. The *lateral eminences*, a pair of bilateral protuberances situated one on either side of the post-chiasmatic eminence. Of these structures the post-chiasmatic, post-infundibular and lateral eminences constitute the *tuber cinereum*, while the infundibular process is appended to the tuber by the infundibular stem. In an earlier paper (8) the writer so interpreted the text and figures published by Retzius (9) as to assign the term eminentia saccularis to the post-chiasmatic eminence. Upon further investigation, however, it became obvious that Retzius referred to what is here called the post-infundibular eminence.

In the attempt to estimate the homological values of the structures in this region of the brain, serial sections obtained from the following adult forms were studied:

Squalus acanthias	Lepus sylvaticus	Canis latrans
Mustelus laevis	Sphingurus prehensilis	Canis familiaris
Lepidosteus osseus	Mephitis mephitica	Genetta vulgaris
Rana pipiens	Odocoelus hemionus	Felis domesticus
Menobranchus	Odocoelus virginianus	Felis pardus
Iguana tuberculata	Oryx beatrix	Felis leo
Gallus gallus	Ovis tragelaphus	Lemur macaco
Botaurus lentiginosus	Ovis aries	Macacus cynomolgus
Didelphys quica	Castor canadensis	Nyctipithecus trivirgatus
Bradypus tridactylus	Mirounga (Macrorhinus angustirostris)	Babuin cynocephalus
Dipus aegypticus		Hylobates hoolock
Dasyprocta agouti	Nasua narica	Simia satyrus
Mus decumanus	Ursus horribilis	Homo

Studies of this portion of the neuraxis in the gross, even with the aid of the binocular, are quite unsatisfactory because of the compact arrangement of the structures which must be examined, and because dissection in this region can scarcely be performed without seriously disturbing the relation of the parts. For this reason, the Born method of reconstruction was employed in the study of the adult cat, dog, rat, rabbit, opossum, common fowl and dog-fish. It was also used in the reconstruction of models which demonstrate the ontogeny of the diencephalic structures in the cat, chick and dog-fish.

ELEMENTS IN THE DIENCEPHALIC FLOOR OF THE ADULT CAT

The lateral view of a model reconstructed to show the left side of the floor of the interbrain in an adult cat is reproduced in figure 2. At its cephalic extremity is the optic chiasm (*4*), while its most caudal structure is the mammillary body (*27*).

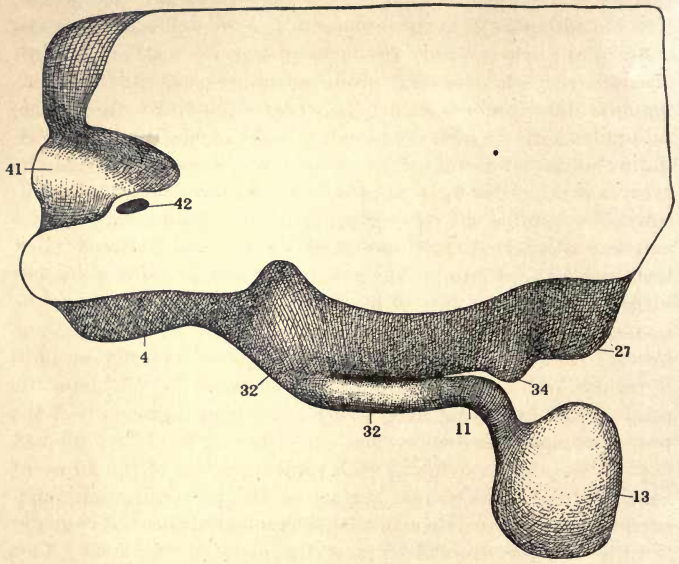

Fig. 2 Lateral view of forebrain reconstruction in adult cat. × 35. The unshaded area shows the cut surfaces of the reconstruction. *4*, chiasm; *11*, infundibular stem; *13*, infundibular process; *27*, mammillary body; *32*, post-chiasmatic eminence; *34*, post-infundibular eminence; *41*, supra-optic crest; *42*, supra-optic recess.

Above the optic chiasm and extending from the median line in either direction along the dorso-cephalic border of the chiasm and optic nerve is a ridge-like elevation, the supraoptic crest (*41*). This ridge is most prominent at and near the median line. It is most conspicuous in the carnivores, especially in the Felidae, but it is present in all the forms examined. The chiasm (*4*)

forms a well defined ridge crossing the outer surface of the floor, but immediately caudal to it is the largest protuberance of this region, the post-chiasmatic eminence or bulbus infundibuli (*32*). It is difficult to demonstrate this eminence on the actual brain, for the reason that it is almost entirely invested by a portion of the pituitary gland, the pars tuberalis. As a rule, this protuberance is torn away with the hypophysis when the attempt is made to study the structures in the floor of the third ventricle and such removal produces an artificial slit-like opening into the ventricle which has been called the *lura*. The post-chiasmatic eminence presents a long ventral surface which slants caudad and ventrad from the optic chiasm; it leaves the general plane of the floor at this level and proceeding for a considerable distance in the direction of the mammillary bodies reaches its greatest prominence about midway between these bodies and the chiasm. The ventral surface presents a shallow furrow whose long axis is in the median plane. This is the *median post-chiasmatic groove*. In this region the neural tissue forming the floor of the eminence is thin. Laterad in both directions the neural tissue rapidly increases in thickness; its ectal surface becoming convex forms two lateral processes of the post-chiasmatic eminence, one on either side of the median post-chiasmatic groove and each projecting free of the adjacent basal surface. The dorsal surface of the post-chiasmatic eminence is, in the main, parallel with its ventral surface but caudally it turns sharply upward to meet the plane of the floor. Two lateral borders bound the eminence, becoming more prominent as they are traced caudad; for about three-quarters of their distance they are divergent; they then become convergent caudad and as they approach each other form with the dorsal and ventral surfaces of the eminence a constricted stem-like prolongation, the infundibular stem (*11*) which projects caudad to become continuous with the expanded infundibular process (*13*). The infundibular stem and the infundibular process are invested by the pars infundibularis of the pituitary gland.

In all the other mammalian forms examined the post-chiasmatic eminence is a prominent feature of the diencephalon; it maintains

its definite relations to the pars tuberalis, and appears with but slight variations in the same general conformation as described in the cat. The most considerable modifications in its form are seen in the anthropoids and man. In these forms it does not hold the same relation to the floor of the interbrain as in the lower mammals. This change is occasioned by the forward and downward rotation which occurs in the hypophysis as the latter sinks into the deepened sella turcica. Another factor operative in this change is the foreshortening of the sella in man and the apes which further tends to force the pituitary gland craniad. The rotation from the developmental standpoint seems to be secondary to the increased depth in the pituitary fossa, for in the five-month human fetus, as the writer has previously shown (8), the post-chiasmatic eminence occupies a position corresponding in all details to that of the adult cat. It is only in the late fetal and early post-natal stages that the protuberance undergoes a change in relations which in effect is the result of a rotation of the hypophysis through 90°. When this is completed the surface described in the cat and other mammals as ventral no longer presents a ventral inclination but is turned craniad, while the eminence as a whole has become elongated in its long axis and constricted transversely. As a result it has a more or less bulbous appearance, a fact which has given rise to the term *bulbus infundibuli*.

The most caudal structures entering into the floor of the third ventricle are the corpora mammillaria (*27*); the one on the left side is shown in figure 2. In the adult cat these bodies are large protuberances situated one on either side of the median line and immediately cephalad to the posterior perforated space. They appear in all the mammals studied and are also present though less conspicuous in sauropsid forms.

The post-infundibular eminence (*34*) occupies a position immediately in front of the mammillary bodies. In lateral view (fig. 2) it does not appear so prominent as the latter structures nor has it the sharp lateral demarcation of the corpora. On the other hand, it is definite in all mammals. So far as may be stated upon the evidence of the material examined it is most

conspicuous in carnivores. In primates it is not always well marked, yet in all the apes examined it was present. In man, especially in later adult life, considerable care may be required to detect it, although in many instances it is quite as evident as in the carnivores; this is particularly true in the brain of the infant and child. The eminence appears in ungulates; at least it was observed in several varieties of artiodactyla (sheep, mountain goat, mule deer, aoudad and Virginia deer). It is prominent in the proboscidea (Indian elephant) and also occurs in rodents and marsupials. The post-infundibular eminence appears as a transverse ridge extending across the ventricular floor. It is most prominent at and near the median line; it presents no sagittal division into bilateral halves and laterally merges with the general plane of the basal region. Its shape is somewhat variable; often it is elongated cephalo-caudad and it may be asymmetrical. Its ventral surface may arise sharply to the floor of the ventricle or it may blend gradually with this area. Its caudal surface usually rises abruptly to the ventricular floor.

The developmental history of the post-chiasmatic eminence shows that it is partially constricted off from the basal portion of the interbrain by the growth of the pars tuberalis of the pituitary gland. Two basal regions thus lie above the eminence, symmetrically placed, one on either side of the median line. In shape they are roughly triangular having their bases turned mesad and their apices projecting laterally. The base of each triangle extends from the post-infundibular eminence almost as far forward as the chiasm. As they are followed laterad each presents a protuberance which is most pronounced near the apex of the triangle. These protuberances and the basal areas with which they are in continuation constitute the lateral eminences (*22*).

The median sagittal view of the model reconstructed from the diencephalic floor in the adult cat is shown in figure 3. This view gives the ventricular recesses many of whose surface expressions have already been discussed. Cephalad to the chiasm (*4*) the ventricular cavity extends forward and slightly down-

ward as the small prechiasmatic recess (*38*) which corresponds to the median portion of the supraoptic crest (*41*). This recess is continued laterad as a long canal extending for some distance above the optic nerve, the supraoptic recess (*42*). Both the prechiasmatic and supraoptic recesses are present in all the forms

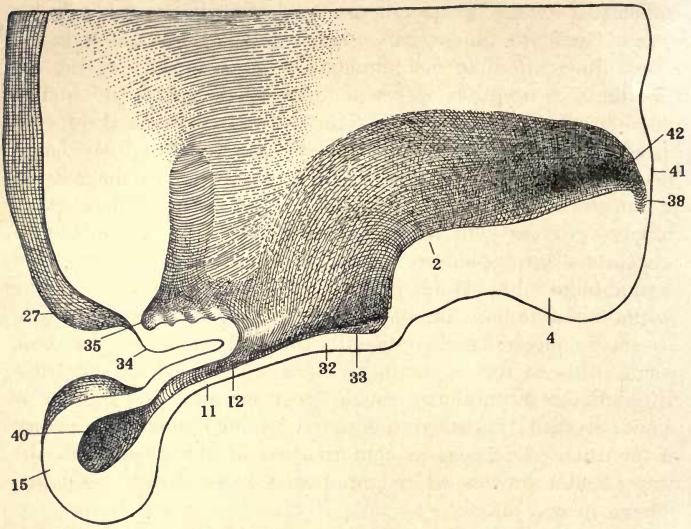

Fig. 3 Mesial view of forebrain reconstruction in adult cat. × 35. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *11*, infundibular stem; *12*, infundibular canal; *15*, infundibular process, pituitary surface; *27*, mammillary body; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *34*, post-infundibular eminence; *35*, post-infundibular recess; *38*, pre-chiasmatic recess; *40*, recess of the infundibular process; *41*, supra-optic crest; *42*, supra-optic recess.

examined. Caudal to the prechiasmatic recess a large prominence rises from the floor of the ventricle in a position corresponding to the optic chiasm. This is the chiasmatic process (*2*). From the caudal extremity of this process the floor falls sharply away and then extends backward for a considerable distance with a marked ventral inclination. The slope thus

formed has its surface expression in the post-chiasmatic eminence and consequently this portion of the ventricular cavity is the post-chiasmatic recess (*33*). This recess extends laterally on either side of the median line forming an expanded portion of the ventricular cavity. As it is followed caudad the post-chiasmatic recess becomes constricted until it forms a tubular canal, the infundibular canal (*12*), which passes through the infundibular stem to communicate with the cavity of the infundibular process, the recessus processi infundibuli (*40*). The post-chiasmatic recess and the infundibular canal were present in all the forms examined but the distance to which the canal penetrates the infundibular stem is variable. In the Felidae it passes through the entire length of the stem while in all other carnivores it extends a short distance only. It is shortest in ungulates, anthropoids and man, although in these forms the infundibular stem attains its greatest length. The recess of the infundibular process is present, so far as I am at present able to state concerning mammals, in the Felidae alone. In these forms it is in direct communication with the third ventricle through the infundibular canal. In such birds and reptiles as I have studied it is present as a cavity having numerous accessory diverticula. The general conformation of this recess and the infundibular process which contains it have already been discussed (page 214).

As the dorsal surface of the post-chiasmatic eminence (*32*) ascends and reaches the plane of the floor, it becomes continuous with an area whose external expression is the ventral surface of the post-infundibular eminence (*34*). Entally this area presents several transverse ridges which separate two or three rather well marked grooves extending transversely across the floor of this region. Caudal to these folds the floor-plate becomes smooth and laterally a conspicuous sinus or recess situated in front of the mammillary recess appears in all the mammals studied. Like several of the other structures already mentioned, it is a most conspicuous element in the Felidae.

THE DIENCEPHALIC FLOOR OF THE ADULT FOWL (GALLUS GALLUS)

All of the eminences appearing in the cat may be identified in the fowl (fig. 4). The supraoptic crest (*41*) is present as a ridge extending laterad along the dorso-cephalic border of the chiasm toward the optic nerve. It marks the position of the supraoptic recess (*42*) of the third ventricle. Caudad to the chiasm the diencephalic floor forms a prominent post-chiasmatic eminence (*32*) which, as in the case of mammals, is invested by the tuberal portion of the pituitary gland and contains the post-chiasmatic recess (*33*). From the caudal extremity of this eminence projects the infundibular stem (*11*) terminating in the infundibular process (*13*). In the bird and the reptile this process presents certain features which distinguish it from that of the mammal. It is broader and each lateral extremity is prolonged to form a slender lateral process (*16*) similar to the lateral process of the selachian. Equally characteristic are the two surfaces of the infundibular process, i.e., the pituitary (*15*) and saccular (*14*) surfaces; the former is in contact with the pituitary gland; the latter has no such relation but presents many irregular convolutions. Its wall is thick and non-vascular. As the saccular surface of the infundibular process ascends and approaches the general plane of the ventricular floor it becomes evaginated to form a diverticulum, the post-infundibular eminence (*34*). This structure seems to present features in which it differs from the post-infundibular eminence in the cat. It appears to be a constituent of the post-chiasmatic eminence rather than being directly in the floor of the ventricle as in mammals. In Botaurus lentiginosus (shown in fig. 5) it more closely resembles the mammalian conditions. The avian third ventricle is in general much more narrow than in other forms. Only in its cephalic extremity does it broaden out to establish free communication with the large prechiasmatic and post-chiasmatic recesses. In the interthalamic portion of the ventricle in the fowl the walls are in close apposition; the extent of the cavity in this region is further limited by the unusual size of the tuberculum postero-superius which projects cephalad for a

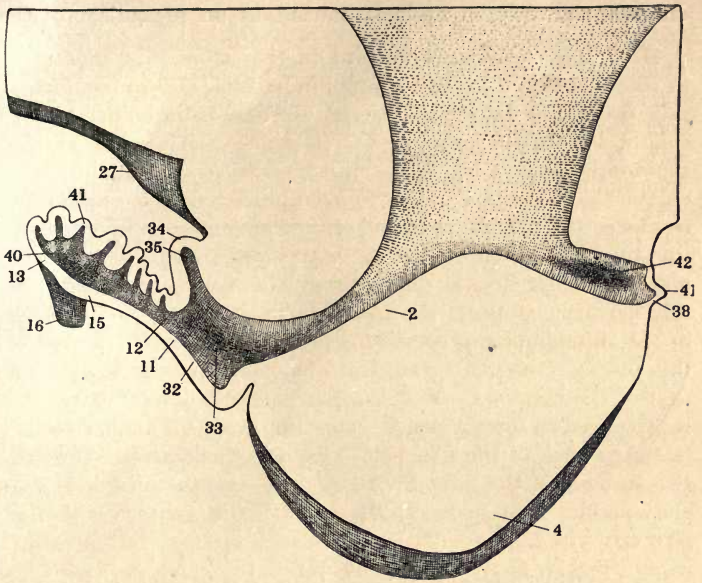

Fig. 4 Mesial view of forebrain reconstruction in adult fowl (Gallus gallus). × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *11*, infundibular stem; *12*, infundibular canal; *13*, infundibular process; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *16*, infundibular process (lateral process); *27*, mammillary body; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *34*, post-infundibular eminence; *35*, post-infundibular recess; *38*, pre-chiasmatic recess; *40*, recess of the infundibular process; *41*, supra-optic crest; *42*, supra-optic recess.

considerable distance into the ventricular chamber. The hypothalamic portion of the ventricle extends caudad beneath the ventral surface of the massive tuberculum postero-superius; for this reason the caudal portion of the post-chiasmatic eminence and the post-infundibular eminence appear to be appendages to rather than constituents in the floor of the third ventricle of the fowl. In the bittern (fig. 5), on the other hand, the post-infundibular eminence is in the ventricular floor while the

infundibular process projects caudad as an appendage of the postchiasmatic eminence. Both the optic chiasm (*4*) and the chiasmatic process (*2*) in the fowl are prominent and the prechiasmatic recess (*38*) is correspondingly deep. In its general features the post-chiasmatic eminence (*32*) is similar to that in the cat. It has a long transverse axis. Its ventral surface presents a longitudinal furrow, the long axis of which is in the median line.

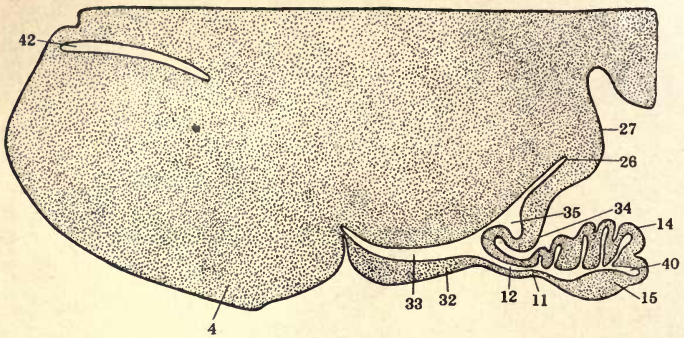

Fig. 5 Sagittal section of Botaurus lentiginosus in region of interbrain. *4*, chiasm; *11*, infundibular stem; *12*, infundibular canal; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *26*, mammillary recess; *27*, mammillary body; *34*, post-infundibular eminence; *35*, post-infundibular recess; *40*, recess of infundibular process; *42*, supra-optic recess.

This is the median post-chiasmatic groove. Here the neural tissue is relatively thin. Extending laterad in both directions from this groove the surface of the eminence becomes convex while the neural tissue rapidly increases in thickness until it forms the prominent lateral processes (*21*) of the post-chiasmatic eminence which project free of the diencephalic floor. The general plane of the post-chiasmatic recess (*33*) is at right angles to the interthalamic portion of the ventricle and follows the ectal contour of the post-chiasmatic eminence. The infundibular canal (*12*) is short and narrow; it communicates directly with the recess of the infundibular process (*40*). The latter presents dorsally a number of minute tubular canals which

project into the corresponding diverticula sacci vasculosi (*6*). These tubular canals open ventrally into a larger subdivision of the recessus processi infundibuli which is in relation to the pituitary surface of the infundibular process, the hypophyseal recess (*10*). Laterally the hypophyseal recess may be traced into the two tapering lateral processes (*16*) of the infundibular process. The post-infundibular recess (*35*) communicates with the post-chiasmatic recess in a position slightly dorsal to the infundibular canal. In the fowl the mammillary bodies (*27*) are partly concealed by the post-infundibular eminence but appear as slight elevations in the floor dorso-lateral to this structure. Because of this relation they seem to be situated at some little distance from the median line on either side having the post-infundibular eminence and its recess interposed between them. They contain no mammillary recess in the fowl. In the bittern the mammillary bodies are dorso-caudad to the post-infundibular eminence and occupy a position much nearer to the median line than in the fowl. A small mammillary recess extends for a short distance into the mammillary body in this form (fig. 5).

THE DIENCEPHALIC FLOOR OF THE ADULT SELACHIAN (MUSTELUS LAEVIS)

The mesial view of a model reconstructed to show the left half of the interbrain floor in the adult Mustelus laevis is reproduced in figure 6. Of the elements entering into the floor the lamina terminalis (*20*) is the most cephalic. The optic chiasm (*4*) is caudal to the supraoptic crest (*41*) which extends transversely across the dorso-cephalic surface of the chiasm, and may be followed for a short distance out upon the optic nerve. Caudal to the chiasm is the post-chiasmatic eminence which differs in certain particulars from the corresponding region of the mammal and sauropsid, although it occupies the same topographical position. The chief points of difference arise from the facts that the three divisions of the post-chiasmatic eminence in the dog-fish are more pronounced than in the

cat and fowl and at the same time this region is a relatively much more expansive area than in the forms already mentioned. Two of its divisions are bilaterally symmetrical in the form of large ovoid protuberances situated one on either side of a smaller median area. The lateral protuberances are the *lobi inferiores* (*21*); they correspond in position to the lateral processes of the

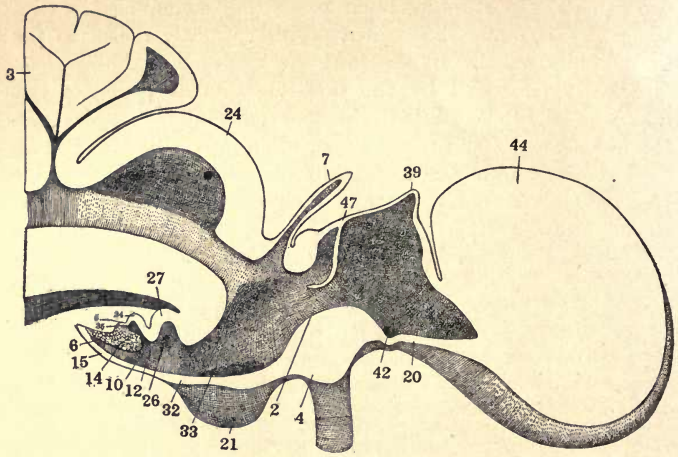

Fig. 6 Mesial view of brain reconstruction in adult Mustelus laevis. × 25. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *3*, cerebellum; *4*, chiasm; *6*, diverticular sacci vasculosi; *7*, epiphysis; *10*, hypophysial recess; *12*, infundibular canal; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *20*, lamina terminalis; *21*, median chiasmatic groove; *24*, mid-brain; *26*, mammillary recess (recess of posterior lobe); *27*, mammillary body (posterior lobe); *32*, post-chiasmatic eminence (inferior lobe); *33*, post-chiasmatic recess (recess of inferior lobe); *34*, post-infundibular eminence; *35*, post-infundibular recess; *39*, paraphysis; *42*, supra-optic recess; *44*, telencephalon; *47*, velum transversum.

post-chiasmatic eminence in birds and mammals; they are not invested by or in contact with the pituitary gland. The small median area corresponds to the median post-chiasmatic groove (*23*); it is contiguous with a relatively long, tongue-like process of the pituitary gland, the developmental history of which latter

gives it all the characteristics of the mammalian and sauropsidan pars tuberalis. In the bird and mammal the caudal extremity of the post-chiasmatic eminence becomes constricted to form the infundibular stem (*11*), but in the selachian this constriction is less marked so that the stem is wide and short. It is difficult to appreciate it at all except by means of reconstruction. At its caudal extremity the stem becomes rapidly expanded to form the spacious infundibular process (*13*). This process presents two characteristic surfaces, i.e., a ventral one which is smooth and in contact with the pituitary gland, the pituitary surface; and a dorsal convoluted saccular surface, membranous in character and highly vascular. This latter forms the *saccus vasculosus*.

Dorsal to the saccus vasculosus is a small protuberance which differs structurally from the saccus in that it is composed chiefly of neural tissue. This is the post-infundibular eminence (*34*), dorsal to which is a larger protuberance, the *posterior lobe* (*27*). This structure forms a prominent eminence at the point of juncture between the mid-brain and the interbrain. Laterally its extremities project free of the adjacent neural tissue. These lateral extremities are in connection with a less protuberant median portion of the lobe. The transverse diameter of the lobus posterior is about twice that of the infundibular eminence; both protuberances are symmetrically disposed with reference to the mid-sagittal plane. Cephalad the recess of the posterior lobe is in direct communication with the diencephalic ventricle; caudad it opens into the post-infundibular recess (*35*). The recess of the infundibular process (*40*) is bounded ventrally by the pituitary surface of the infundibular process, while caudo-dorsally it is limited by the saccular surface forming the saccus vasculosus. This surface is thrown into a number of convoluted folds thus producing the diverticula sacci vasculosi (*6*). Ventral to the saccus vasculosus the infundibular recess presents a marked subdivision, the hypophyseal recess (*10*), while both the pituitary and saccular surfaces are so prolonged laterad as to form two long tapering processes, each of which contains a lateral extension of the infundibular recess. Corre-

sponding to the short, broad infundibular stem, the infundibular canal (*12*) is not well defined, although it may be recognized as a slight constriction occurring dorsad at the area of transition between the saccus vasculosus and the post-infundibular eminence and ventrad in the region in which the pituitary surface of the infundibular process passes into the median post-chiasmatic groove (*23*). The post-chiasmatic recess (*33*) corresponds in its subdivisions to the post-chiasmatic eminence, there being two large lateral diverticula extending into the inferior lobes in connection with a median canal which communicates cephalad with the suprachiasmatic portion of the third ventricle and caudad with the recess of the infundibular process. Cephalad to the post-chiasmatic eminence the ventricular floor is elevated above the chiasm to form the chiasmatic process (*2*) which passes across the floor as a prominent transverse ridge. The dorso-cephalic surface of this ridge becomes rapidly depressed as it proceeds cephalad, and in the mid-sagittal plane becomes the caudal boundary of the prechiasmatic recess (*38*).

Traced laterad this recess leads into a small tubular canal which extends for some distance above the optic nerve, the supraoptic recess (*42*). In the selachian the lamina terminalis (*20*) occupies a nearly horizontal plane, extending with a slight dorsocephalic inclination from the prechiasmatic recess to the corpus striatum.

EMBRYOLOGICAL ANALYSIS OF THE DIENCEPHALIC FLOOR IN THE CAT, CHICK AND DOG-FISH

The following analysis of the floor of the interbrain is based upon some recent work of Prof. H. von W. Schulte (12), in which the writer collaborated.[1] It is shown in this study that the forebrain in the cat consists of two primitive elements, the optic vesicles and the mammillary region. The latter persists with but little alteration until a relatively late period. The primi-

[1] In connection with this work it gives me pleasure to express my indebtedness to Professor Schulte for, although it was my privilege to collaborate with him in the study of the early development of the brain in the domestic cat, the new ontogenetic interpretation resulting from this investigation originated with him.

tive optic vesicles early become profoundly remodelled giving rise to a much reduced optic evagination and a pronounced area of the neural wall which surrounds it. This area is called the *ectoptic zone*. It presents itself as an arc of three distinct segments, the dorsal segment giving rise to the thalamencephalon, the cephalic segment to the telencephalon and the ventral segment to the infundibular region. All of these secondary derivatives are present in the cat embryo of twenty-one somites (see fig. xxxviii in loc. cit.).

Development of the diencephalic floor of the cat

Cat embryo of 4.5 mm.; twenty-six somites; Specimen No. 495 (fig. 7). The forebrain of this embryo shows an advance over the conditions observed in the embryo of twenty-one somites. All of the primitive elements of the prosencephalon previously described may be recognized. The optic vesicles (*29*) are further reduced in size, and present a constriction at their point of attachment to the neural tube. Their external configuration is still convex upon all surfaces. The ectoptic zone shows its characteristic division into thalamencephalon (*43*), telencephalon (*44*) and infundibular region (*17*). The regio mammillaris (*25*) is well marked and ectally separated from the apex of the infundibular region by a shallow transverse furrow, the tubercle of the floor (*46*).

The most pronounced changes are evident in the regio infundibularis, not only in the fact that this region is enlarged but also because it presents two subdivisions, both evolved from the apex of this area. The first of these subdivisions appears as a ventral protrusion which is conical in shape, the infundibular evagination (*18*). Dorsal and caudal to this appears a large, shallow diverticulum which, because of its position, may be designated the post-infundibular evagination (*36*). The remainder of the infundibular region forms the greater part of the floor of the prosencephalic ventricle. Its general plane of inclination is caudo-ventral, and its thickness is uniform throughout its entire extent. Entally it presents on either side a deep groove passing along the lateral wall from the now circular orifice of the optic

vesicle to the apex of the infundibular region. This is the optico-infundibular groove (*31*). It occupies relatively the same position as the horizontal limb of the primitive optic sulcus. Its increased prominence upon the ental surface of the ventricular wall appears to have occasioned a corresponding ridge upon the ectal surface, the optico-infundibular ridge.

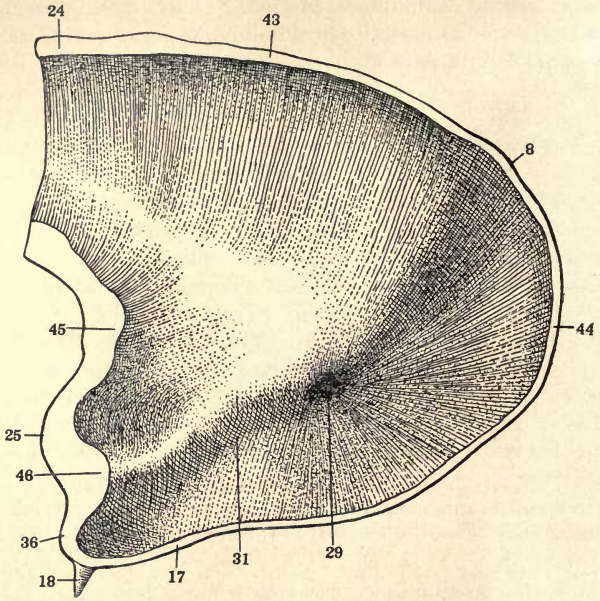

Fig. 7 Mesial view of forebrain reconstruction of a 4.5 mm. cat embryo (26 somites). × 150. The unshaded area shows the cut surfaces of the reconstruction. *8*, ectoptic zone of Schulte; *17*, infundibular region; *18*, infundibular evagination; *24*, mid-brain; *25*, mammillary evagination; *29*, optic evagination; *31*, optico-infundibular groove; *36*, post-infundibular eminence; *43*, thalamencephalon; *44*, telencephalon; *46*, tubercle of the floor of Schulte.

The mammillary region, although increased in size as compared with the earlier stages, manifests no other changes. Dorsal to it is the tuberculum postero-superius (*45*), while ventrad is

the floor tubercle of Schulte (*46*), the tuberculum postero-inferius.

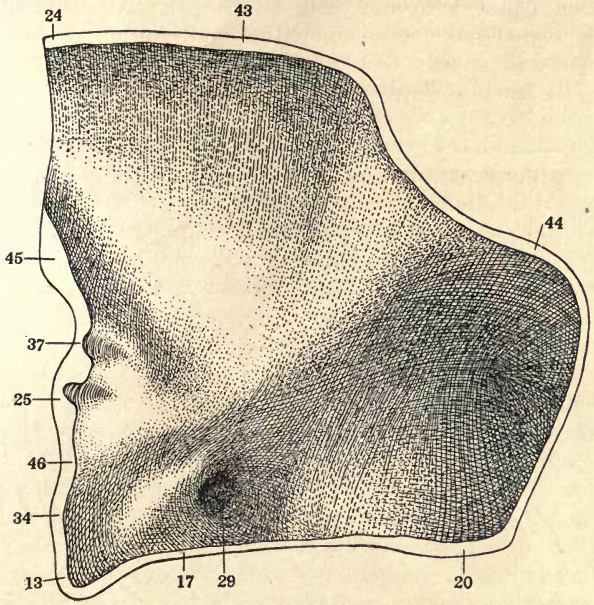

Fig. 8 Mesial view of forebrain reconstruction of 7 mm. cat embryo. × 100. The unshaded area shows the cut surfaces of the reconstruction. *13*, infundibular process; *17*, infundibular region; *20*, lamina terminalis; *24*, mid-brain; *25*, mammillary region; *29*, optic evagination; *34*, post-infundibular eminence; *37*, post-mammillary evagination; *43*, thalamencephalon; *44*, telencephalon; *45*, tuberculum postero-superius; *46*, tubercle of the floor of Schulte.

Cat embryo of 7 mm.; Specimen No. 266 (*fig. 8*). Changes in this embryo have occurred both in the mammillary and infundibular regions. The former now shows a subdivision into what must be considered the mammillary recess (*26*), and dorsal to this a smaller evagination, the post-mammillary recess (*37*). Both of these evaginations affect the median plane, while in the mammillary area two lateral diverticula have appeared, the anlages of the mammillary bodies.

The subsequent history of the post-mammillary evagination shows that this recess is involved in the development of the corpus interpedunculare. In the infundibular region, the optico-infundibular ridge is much less prominent and the entire region is increased in size. Its notable characteristics at this stage are a large infundibular process (*13*) and a prominent post-infundibular eminence (*34*).

The infundibular evagination now contains an extension of the prosencephalic ventricle, in this respect differing from the conditions in the 4.5 mm. embryo in which the infundibular process is solid and as yet contains no ventricular extension.

The optic vesicle (*29*) presents a distinct cupping upon its latero-cephalic surface and is continuous with the lateral wall of the prosencephalon by means of a constricted stem, the optic peduncle (*30*). Along the cephalic surface of this peduncle runs a shallow groove, which becomes expanded as it passes out upon the latero-cephalic surface of the cup. Entally a groove connects the canal of the two optic stems across the floor of the prosencephalon. This is the interoptic groove. Cephalad as well as caudad to this groove the floor is thin. In this stage, therefore, the remodelling of the floor has resulted in the subdivision of the mammillary region, forming the mammillary and post-mammillary evaginations, while laterally the anlages of the mammillary bodies have become defined. The infundibular region likewise shows an advance in its subdivisions, i.e., the infundibular process (*13*) and the post-infundibular eminence (*34*). The rest of the infundibular regions still remains in the general plane of the prosencephalic floor.

Cat embryo of 10 mm.; Specimen No. 498 (fig. 9). The changes in this stage are more evident in the telencephalon and thalamencephalon than in the floor-plate. The optic cup is now more pronounced than in the earlier stage, the optic stem still more constricted.

Entally a well marked interoptic groove (*19*) is present, and immediately caudal to this the floor-plate is thickened to form the interoptic torus. The floor of the infundibular region from the torus to the infundibular evagination is thin. The infundib-

ular evagination shows a constriction at its point of junction with the infundibular region, in this way demarcating the definitive infundibular stem (*11*) and the infundibular process (*13*). The ventricular cavity extends through the narrow in-

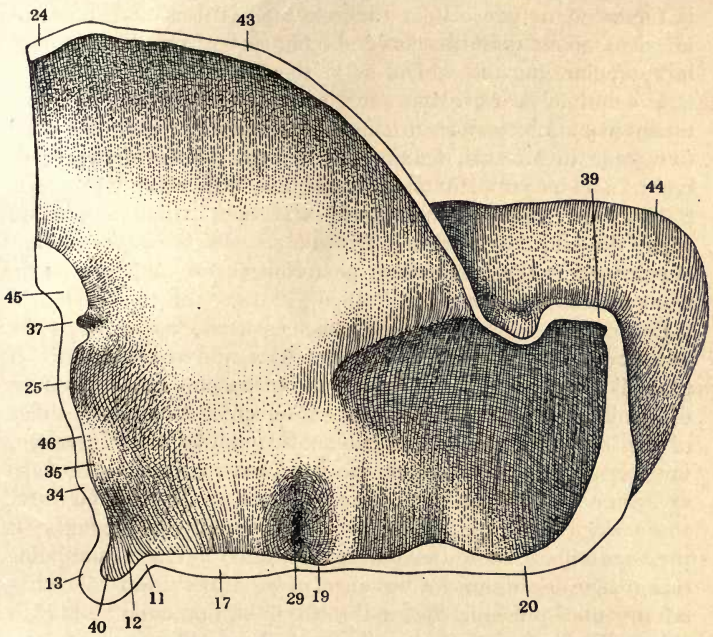

Fig. 9 Mesial view of forebrain reconstruction of 10 mm. cat embryo. × 100. The unshaded area shows the cut surfaces of the reconstruction. *11*, infundibular stem; *12*, infundibular canal; *13*, infundibular process; *17*, infundibular region; *19*, inter-optic groove; *20*, lamina terminalis; *24*, mid-brain; *25*, mammillary region; *29*, optic evagination; *34*, post-infundibular eminence; *35*, post-infundibular recess; *37*, post-mammillary evagination; *39*, paraphysis; *40*, recess of the infundibular process; *43*, thalamencephalon; *44*, telencephalon; *45*, tuberculum postero-superius; *46*, tubercle of the floor of Schulte.

fundibular process, thus giving rise to the infundibular canal (*12*) and the infundibular recess (*40*). Dorsal to the infundibular stem the floor of the ventricle shows a large post-infundibular evagination, which from this time maintains the same general

relation to the infundibular process and for this reason may be designated the post-infundibular eminence (*34*). The cavity of this eminence which communicates with the third ventricle forms the post-infundibular recess (*35*). A slight ridge which is the remnant of the floor tubercle (*46*) (tuberculum postero-inferius) separates the post-infundibular recess from the mammillary evagination (*26*) which, as in the 7 mm. embryo, presents two subdivisions affecting the mid-sagittal plane, i.e., the mammillary and post-mammillary evaginations; while laterally two large diverticula defining the anlages of the mammillary body have increased in prominence but still retain an ample recess, the recessus mammillaris, which is in communication with the third ventricle. Dorsal to the post-mammillary evagination is the tuberculum postero-superius (*45*) now somewhat increased in size.

Cat embryo of 12 mm.; Specimen No. 217 (fig. 10). The advance in this embryo over that of 10 mm. appears in the fact that all the definitive elements of the diencephalic floor are now discernible. The most conspicuous changes affect the region of the interoptic groove and the area caudal to it. Where this optic groove formerly appeared as a furrow extending between the orifices of the optic peduncles, the floor is still relatively thin; but caudal to this groove, both entally and ectally, it presents a pronounced thickening, the ectal increase in size being due to the beginning formation of the optic chiasm (*4*), while entally the thickening forms the chiasmatic process (*2*). Thus the furrow in front of the process becomes the prechiasmatic recess (*38*). Ascending from the latter the lamina terminalis (*20*) extends obliquely cephalo-dorsad to join the roof-plate. Quite as notable as the changes which have occurred in the region of the chiasm are those which appear in the area immediately caudad to it. Here the diencephalic floor, without increasing in thickness, presents a ventral protrusion which forms the post-chiasmatic eminence (*32*). This eminence is symmetrically disposed with reference to the mid-sagittal line. Caudal to this is the infundibular stem (*11*) considerably lengthened and expanding to form the infundibular process (*13*). Between the

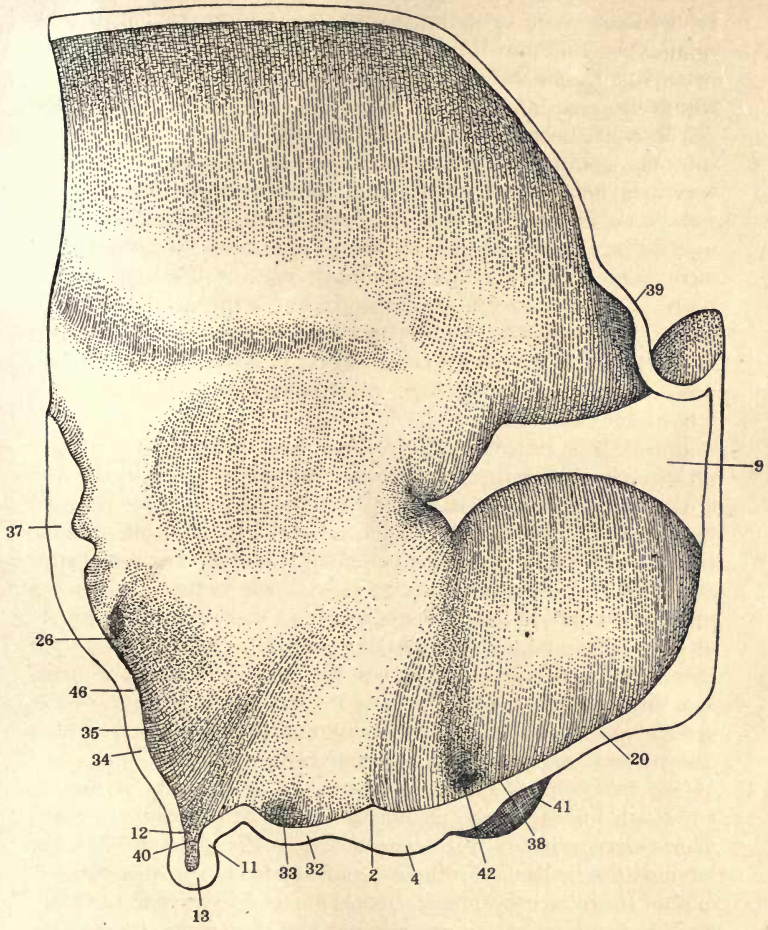

Fig. 10 Mesial view of forebrain reconstruction of 12 mm. cat embryo. × 100. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *9*, foramen of Monro; *11*, infundibular stem; *12*, infundibular canal; *13*, infundibular process; *20*, lamina terminalis; *26*, mammillary recess; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *34*, post-infundibular eminence; *35*, post-infundibular recess; *37*, post-mammillary evagination; *38*, pre-chiasmatic recess; *41*, supra-optic crest; *42*, supra-optic recess.

infundibular stem and the mammillary evagination (*26*) is a small but distinct diverticulum of the floor appearing as a prominence upon the ectal surface and forming the post-infundibular eminence (*34*).

The mammillary evagination is still large and its cavity spacious. In it may still be recognized the subdivisions already described, i.e., the two lateral evaginations of the mammillary bodies, the median mammillary evagination (*26*) and the post-mammillary evagination (*37*). All of the eminences mentioned have their corresponding recesses, i.e., the post-chiasmatic recess (*33*), the post-infundibular recess (*35*), the mammillary recess (*26*) and the post-mammillary recess. The ventricle extends through a short and narrow infundibular canal (*12*) into a relatively large recess of the infundibular process.

The eye-cup in this stage is now completely formed. It is attached to the prosencephalon by the optic peduncle; but certain changes have occurred in this peduncle which have important bearings upon the structures evolved from it. As the peduncle approaches the brain-wall it becomes rapidly expanded in the form of a distinct evagination of the prosencephalon, into which extends an expansion of the ventricle. Ventral to this evagination the optic peduncle has increased in thickness, due to the appearance of fibers forming the optic nerve and entering the optic chiasm (*4*). In this manner a diverticulum of the third ventricle comes to overlie the lateral portion of the optic chiasm and the proximal portion of the optic nerve. This diverticulum is the supraoptic recess (*42*).

Cat embryo of 15 mm.; Specimen No. 505 (*fig. 11*). In this embryo a foreshortening has occurred in the diencephalic floor. This is due principally to the change in the inclination of the lamina terminalis (*20*) which is now vertical. In consequence of this alteration the prechiasmatic recess has become the most cephalic portion of the ventricle. The chiasmatic process (*2*) and the chiasm have increased in size. The post-chiasmatic eminence is still further expanded and its recess is larger. The post-infundibular eminence (*34*) occupies a typical position between the infundibular stem (*11*) and the mammillary evagi-

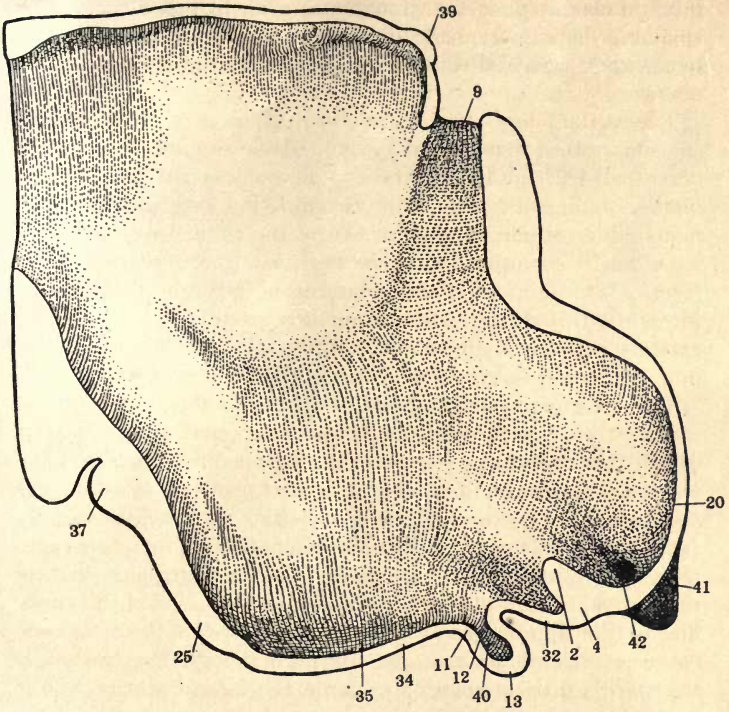

Fig. 11 Mesial view of forebrain reconstruction of 15 mm. cat embryo × 75. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *11*, infundibular stem; *12*, infundibular canal; *13*, infundibular process; *20*, lamina terminalis; *25*, mammillary region; *32*, post-chiasmatic eminence; *34*, post-infundibular eminence; *35*, post-infundibular recess; *37*, post-mammillary evagination; *40*, recess of infundibular process; *41*, supra-optic crest; *42*, supra-optic recess.

nation (*26*). In this latter evagination is possible to recognize a median, a post-mammillary and two lateral recesses. The infundibular stem has increased in length so that the infundibular canal (*12*) is longer, while the infundibular process shows a distinct thickening along its ventro-cephalic surface, thus

giving evidence that the growth going on in this structure at this stage is in a cephalic direction. The optic peduncle has increased in size, due to the addition of more optic fibers.

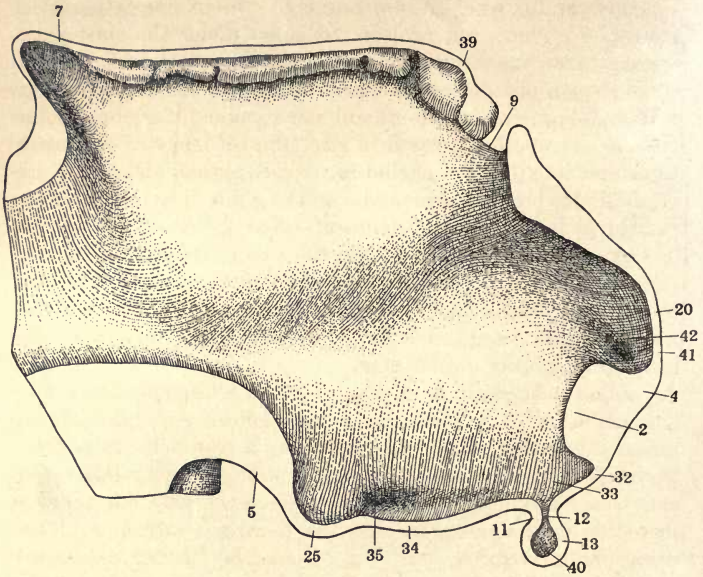

Fig. 12 Mesial view of forebrain reconstruction of 30 mm. cat embryo. × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *5*, corpus interpedunculare; *7*, epiphysis; *9*, foramen of Monro; *11*, infundibular stem; *12*, infundibular canal; *13*, infundibular process; *20*, lamina terminalis; *25*, mammillary region; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *34*, post-infundibular eminence; *35*, post-infundibular recess; *39*, paraphysis; *40*, recess of the infundibular process; *41*, supra-optic crest; *42*, supra-optic recess.

Cat embryo of 30 mm.; Specimen No. 585 (fig. 12). The foreshortening of the diencephalic floor observed in the embryo of 15 mm. is here less pronounced, although the lamina terminalis (*20*) retains its vertical position. The prechiasmatic and supra-optic recesses are more pronounced, due to the increase in size of the chiasmatic process (*2*). The chiasmatic fibers are present in large numbers in the ventral aspect, while the dorsal extension

of the chiasmatic process appears to be due to the presence of increasing numbers of commissural fibers. The post-chiasmatic eminence (*32*) has increased in size, both in the median line as well as laterally, where it now begins to present free extremities. Its recess is deep and projects cephalad under the chiasmatic process in such a way that coronal sections of the brain in this stage show a distinct recess which extends forward beneath the chiasmatic process. The infundibular stem and the infundibular process have both increased in size; the tendency of the latter to extend its growth cephalad has about ceased, and the entire infundibular process seems to be on the point of swinging dorso-caudad in its further development. The general shape of the process at this stage is oval, and the two relatively long lateral processes appear on either side. The infundibular canal (*12*) is relatively longer and the recess of the infundibular process not only more spacious but more definitely demarcated from the canal than in any earlier stage.

Caudad to the infundibular stem (*11*) is a large post-infundibular eminence (*34*) containing a well defined post-infundibular recess (*35*), which latter is separated by a transverse ridge from the mammillary recess. The neural wall bounding this recess and thus forming the mammillary eminence (*27*) has notably increased in thickness, so that the relative dimensions of the diencephalic ventricle are being lessened by the encroachment due to the thickening of the brain floor in the region of the mammillary bodies. This thickening particularly affects the two lateral mammillary diverticula, while the median mammillary and post-mammillary evaginations are no longer discernible. Thickening has also occurred in the region of the post-mammillary evagination, and this area now shows an ectal protuberance marking the site of the corpus interpedunculare (*5*).

Cat embryo of 51 mm.; Specimen No. 104 (fig. 13). The changes observed in this stage involve the further development of the chief tendencies observed in the 30 mm. embryo, i.e., the pronounced caudal deflection of the infundibular process (*13*) which appears as a distinct appendage to the floor of the ventricle, due to the increased length and constriction of the infundibular stem (*11*). This process now presents two surfaces, one which faces

cephalad and is relatively thick and the other which faces caudad and is thin. Both of these surfaces are closely invested by the pars infundibularis of the pituitary gland and their continuation laterad produces two long and slender lateral processes. The

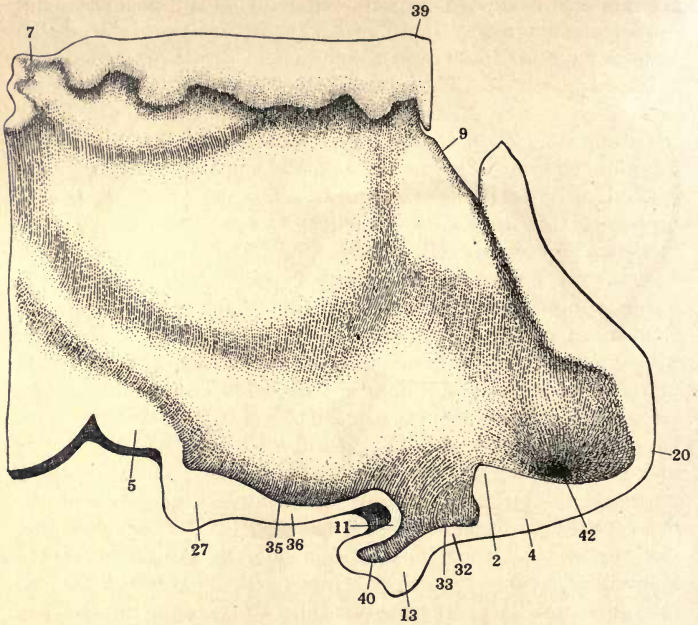

Fig. 13 Mesial view of forebrain reconstruction of 51 mm. cat embryo. × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *5*, corpus interpedunculare; *7*, epiphysis; *9*, foramen of Monro; *11*, infundibular stem; *13*, infundibular process; *20*, lamina terminalis; *27*, mammillary body; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *35*, post-infundibular recess; *36*, post-infundibular evagination; *39*, paraphysis; *40*, recess of the infundibular process; *42*, supra-optic recess.

brain floor in the mammillary region is still further increased in thickness and two definite lateral protuberances, one on either side of the median line, have made their appearance. Because of the increased thickness of the neural tissue which bounds them the lateral diverticula of the mammillary recess have

greatly decreased in size and seem to be on the point of disappearing.

The median mammillary and post-mammillary evaginations are no longer recognizable, but a protuberance marking the position of the corpus interpedunculare (*5*) is still defined as the

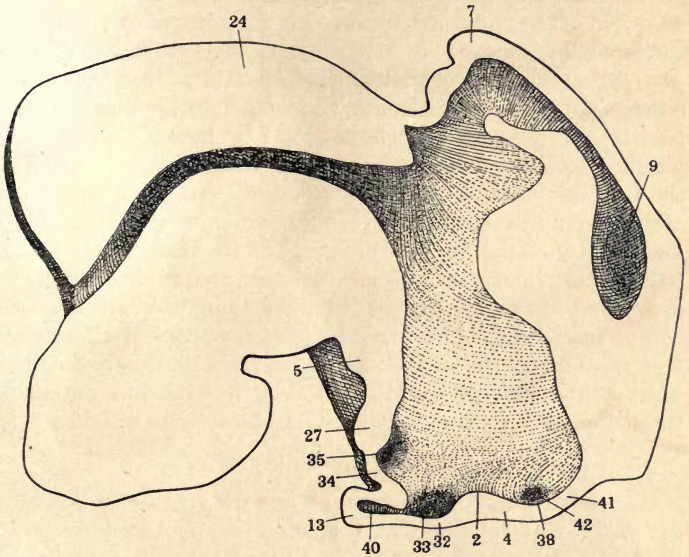

Fig. 14 Mesial view of forebrain reconstruction of 70 mm. cat embryo. × 25. The unshaded area shows the cut surface of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *5*, corpus interpedunculare; *13*, infundibular process; *27*, mammillary body; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *34*, post-infundibular eminence; *35*, post-infundibular recess; *38*, pre-chiasmatic recess; *40*, recess of infundibular process; *41*, supra-optic crest; *42*, supra-optic recess.

thickened area in that part of the floor. The other eminences and recesses defined in the earlier stages are all present with but slight changes.

Cat embryo of 70 mm.; Specimen No. E 70 (fig. 14). In its main outlines the diencephalic floor at this stage has attained its adult conformation. It is not, however, disposed in the

ultimate plane of the floor as yet, for the region of the post-infundibular and mammillary areas has assumed a more vertical position than is true of the 15, 30 and 51 mm. stages and this position will later be so modified in attaining adult conditions that the most dorsal element in this region, the corpus interpedunculare (*5*), will be rotated ventrad through an arc of nearly 90°. All of the eminences observed in the early stages and their corresponding recesses are here present. The infundibular process (*13*) presents two well marked, lateral processes, one on either side; the post-chiasmatic eminence (*32*) likewise presents two lateral processes which project free beneath the suprajacent lateral eminences of the tuber cinereum. The wall of the post-infundibular eminence (*34*) has increased in thickness and it bounds a spacious post-infundibular recess (*35*). Two mammillary bodies are now present, but the mammillary recess (*26*) cannot be defined because of the thickening which has progressed in the development of the mammillary region. The corpus interpedunculare (*5*) forms the most dorsal element in this portion of the ventricular floor; the prechiasmatic and supraoptic recesses (*38* and *42*), the latter extending out upon the optic nerve for some distance, are both present.

Development of the diencephalic floor in the chick

Chick of twenty-three hours; eight somites; Specimen No. 618 (fig. 15). The forebrain at this stage consists exclusively of the large optic vesicles similar in all respects to the vesicles in the cat, although their transverse diameter is greater and their altitude less. Entally the horizontal segment of the optic sulcus is well defined, extending from the deepest portion of the optic evagination (*29*) obliquely meso-caudad and converging with the corresponding sulcus of the opposite side. The angle formed by the convergence of these two sulci is occupied by a clearly defined prominence, the tubercle of the floor (*46*). The neuropore (*28*) is still open for a considerable distance at the cephalic extremity of neural folds, but its closure is more advanced than in the cat embryo of eight somites.

Chick of forty-nine hours; twenty somites; Specimen No. 619 (fig. 16). The advances in this stage consist in the reduction

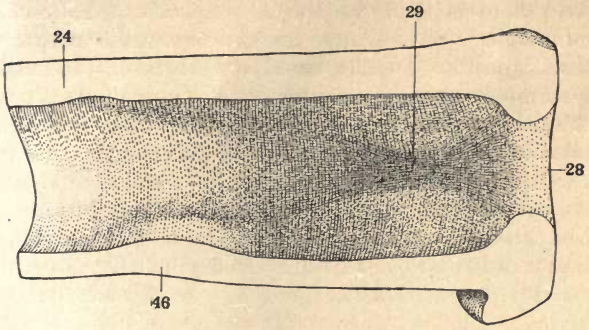

Fig. 15 Mesial view of forebrain reconstruction of 8 somite chick. × 150. The unshaded area shows the cut surfaces of the reconstruction. *24*, mid-brain; *28*, neuropore; *29*, optic evagination; *46*, tubercle of the floor of Schulte.

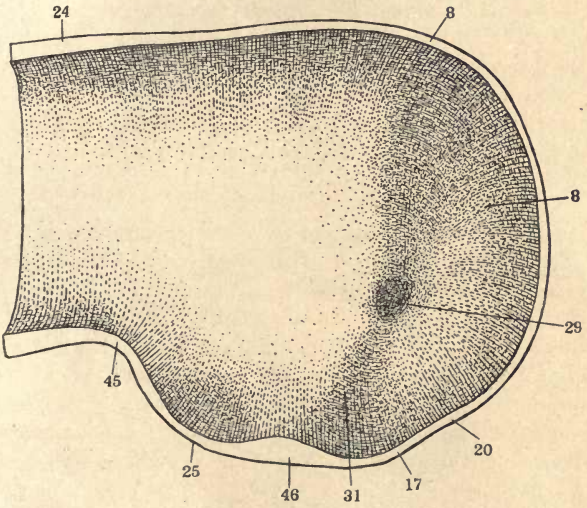

Fig. 16 Mesial view of forebrain reconstruction of 20 somite chick. × 150. The unshaded area shows the cut surfaces of the reconstruction. *8*, ectoptic zone of Schulte; *17*, infundibular region; *20*, lamina terminalis; *24*, mid-brain; *25*, mammillary region; *29*, optic evagination; *31*, optico-infundibular groove; *46*, tubercle of the floor of Schulte.

of the primitive optic vesicles (*29*) and the formation of the ectoptic zone (*8*) which now presents its dorsal, cephalic and ventral segments. Further advance is found in the formation of a definite mammillary region (*25*). The boundary between midbrain and forebrain is indicated by the tuberculum postero-superius (*45*). The ventral segment of the ectoptic zone appears as a well defined infundibular region (*17*) and a wide, shallow groove extends from the orifice of the optic evagination to the apex of this region, forming the optico-infundibular groove (*31*). A slight transverse ridge separates the mammillary and infundibular regions thus marking the position of the tubercle of the floor

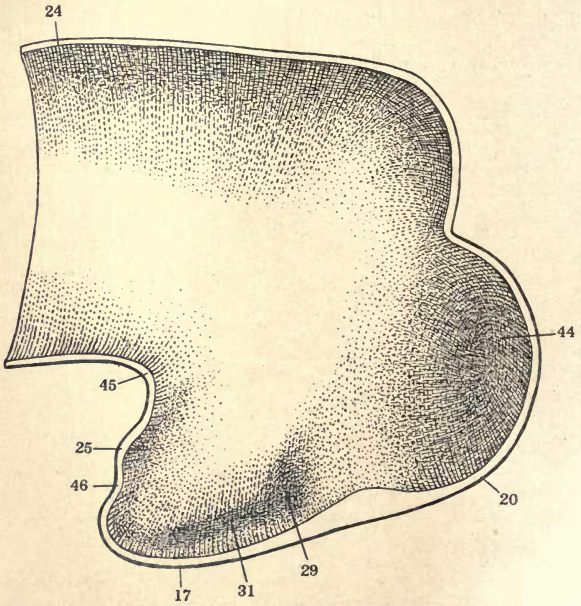

Fig. 17 Mesial view of forebrain reconstruction of 6.75 mm. chick. × 150. *17*, infundibular region; *20*, lamina terminalis; *24*, mid-brain; *25*, mammillary region; *29*, optic vesicle or evagination; *31*, optico infundibular groove; *44*, telencephalon; *45*, tuberculum postero-superius; *46*, tubercle of the floor of Schulte.

(*46*). Ectally the mammillary and infundibular regions present distinct eminences.

Chick of 108 hours; 6.75 mm.; Specimen No. 371 (fig. 17). The tendency of the infundibular region (*17*) to assume a more ventral relation with reference to the mammillary region is here more pronounced. Otherwise, with the exception of the greater

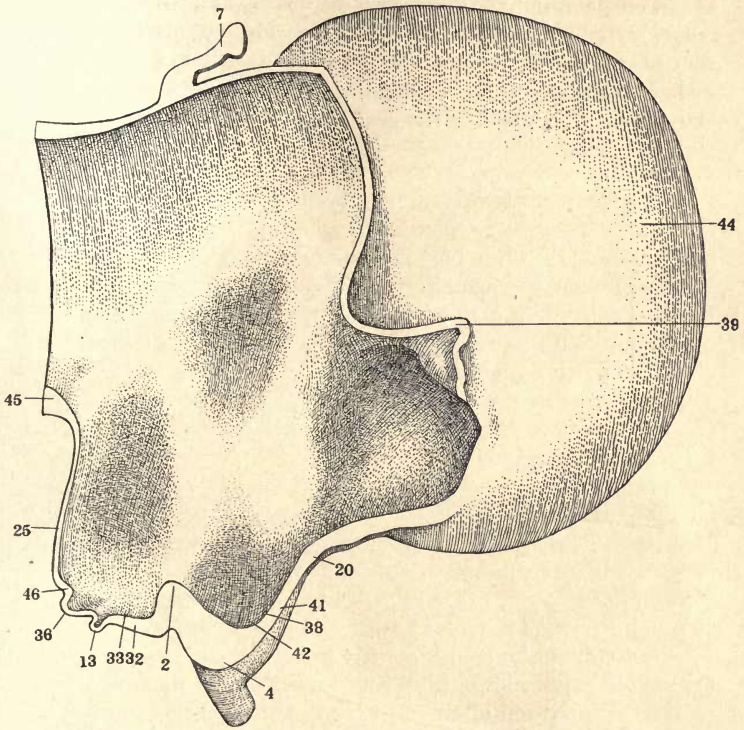

Fig. 18 Mesial view of forebrain reconstruction of chick of 5 days and 20 hours. × 100. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *7*, epiphysis; *13*, infundibular process; *20*, lamina terminalis; *25*, mammillary region; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *36*, post-infundibular eminence; *38*, pre-optic recess; *39*, paraphysis; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon; *45*, tuberculum postero-superius; *46*, tubercle of the floor of Schulte.

reduction of the optic vesicles, there are no notable changes in this stage.

Chick of five days, twenty hours; Specimen No. 326 (fig. 18). In this stage a marked change has occurred in the infundibular region (*17*) namely, the appearance of two distinct evaginations at the apex of this region, the more ventral of which is involved in the formation of the infundibular process (*13*), while the more dorsal one ultimately forms the post-infundibular eminence (*34*). These two evaginations of the infundibular region are more pronounced in the chick than in either the cat or the dog-fish. The mammillary region (*25*) has increased in size, but occupies a position dorsal to the infundibular region as in the immediately preceding stage. The mammillary recess (*26*) is correspondingly larger. Thus the floor of the third ventricle now presents three separate evaginations, the infundibular evagination (*18*), the post-infundibular evagination (*36*) and the mammillary evagination (*26*), a condition corresponding in all details to the early history of the development in the mammillary and infundibular regions of the cat. At this stage also a large chiasmatic process (*2*) has appeared thus demarcating a prechiasmatic recess (*38*) and a post-chiasmatic recess (*33*). This latter recess is marked upon the exterior surface by a prominent post-chiasmatic eminence (*32*).

Chick of eight days; Specimen No. 315 (fig. 19). In this stage all of the definitive elements of the diencephalic floor are present. The chiasm (*4*) and the chiasmatic process (*2*) have increased in size with the consequence that the prechiasmatic and post-chiasmatic recesses (*38* and *33*) are more pronounced. The supraoptic crest (*41*) and supraoptic recess (*42*) are both present. The post-chiasmatic eminence (*32*) has also increased in prominence. It now shows a distinct longitudinal furrow which marks the inception of the median post-chiasmatic groove. In the region of this groove the floor is relatively thin, while upon either side of it the neural tissue has a considerable thickness. In the caudal portion of the infundibular region the dorsal and ventral evaginations are more marked than in the next earlier stage and in them may be distinguished the anlages of the infundibular process (*13*) and post-infundibular eminence (*34*).

The infundibular process manifests a tendency toward the development of a short infundibular stem (*11*) while at the sides it gives the first evidence of its lateral processes (*16*). The mammillary region presents two large lateral processes and a smaller median recess with surface markings corresponding with these evaginations. The mammillary recess (*26*) as a whole is gradually being reduced, due to a thickening of its lateral walls.

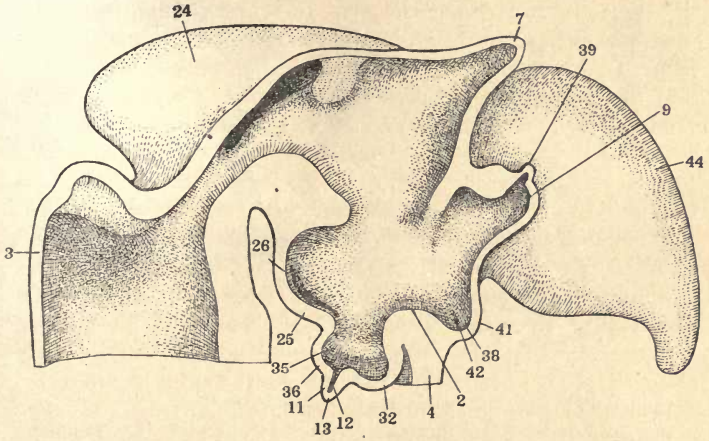

Fig. 19 Mesial view of forebrain reconstruction of chick of 8 days. × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *3*, cerebellum; *4*, chiasm; *7*, epiphysis; *9*, foramen of Monro; *11*, infundibular stem; *12*, infundibular canal; *13*, infundibular process; *16*, infundibular process (lateral process); *24*, mid-brain; *25*, mammillary region; *26*, mammillary recess; *32*, post-chiasmatic eminence; *36*, post-infundibular eminence; *38*, pre-chiasmatic recess; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon.

Chick of nine days, nineteen hours; Specimen No. 919 (fig. 20). The reconstruction of this stage shows no material change in the supraoptic crest (*41*), supraoptic and prechiasmatic recesses (*42* and *38*). The chiasmatic process (*2*) is less prominent than in the eight-day chick, although the chiasm (*4*) has increased relatively in size. Caudal to the chiasm the post-chiasmatic eminence (*32*) has gained somewhat in prominence. It now

shows clearly the median post-chiasmatic groove and the two lateral processes, one on either side of this groove. More marked is the change in the caudal portion of the infundibular region where the infundibular process is now well formed, and connected with the floor of the diencephalon by a short, broad stalk, the infundibular stem (*11*). The infundibular process itself

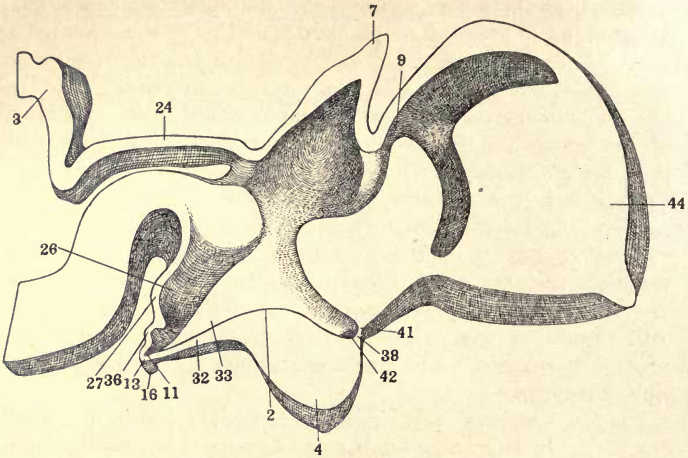

Fig. 20 Mesial view of forebrain reconstruction of chick of 9 days and 19 hours. × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *3*, cerebellum; *4*, chiasm; *7*, epiphysis; *9*, foramen of Monro; *11*, infundibular stem; *13*, infundibular process; *24*, mid-brain; *26*, mammillary recess; *27*, mammillary body; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *36*, post-infundibular eminence; *38*, pre-chiasmatic eminence; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon.

presents a median expanded portion, from which there extends to either side a slender lateral process. This formation corresponds closely to the conditions in the infundibular process of Mustelus at the stage of 50 mm. The ventricular cavity extends through the infundibular stem and upon entering the infundibular process rapidly expands into a number of branching diverticula. These diverticula are confined largely to the dorsal surface of the infundibular process and extend from its median

portion into the lateral processes. At this stage, therefore, it is possible to distinguish between a dorsal or saccular surface and a ventral surface, the latter being in contact with the anlage of the pituitary gland.

Dorsal to the stem of the infundibular process is a small evagination corresponding in its general relations to the part already described as the anlage of the post-infundibular eminence (*36*). Its growth has been less pronounced than that of the other parts of the infundibular region. The cavity of the third ventricle extends into it forming the post-infundibular recess (*35*). In the mammillary region (*25*) the tendency toward the reduction of the ventricular cavity already noted in the chick of eight days has proceeded still further. The mammillary region itself forms a large protuberance dorsal to the post-infundibular eminence. The lateral median evaginations are still prominent on the surface, but the cavities contained in them have been greatly reduced now forming small accessory recesses connected with the third ventricle. The median mammillary recess (*26*) is still prominent sagittally, although its transverse diameters are much reduced. The mammillary bodies are now defined upon the surface.

Chick of fourteen days, eighteen hours; Specimen No. 1418 (fig. 21). In this stage adult conditions have practically been attained. The post-chiasmatic eminence (*32*) is less prominent with the result that the prechiasmatic recess (*38*) is less well defined. Traced laterad, however, this recess may be followed into a small canal overlying the chiasm and proximal portion of the optic nerve, the supraoptic recess (*42*). The position of this recess is marked upon the surface by the supraoptic crest (*41*). In the infundibular region the post-chiasmatic eminence is well defined; its median post-chiasmatic groove (*23*) as well as its two lateral processes are prominent. The caudal portion of the infundibular region shows but little change. The main portion of the infundibular process is somewhat larger; its dorsal convoluted surface is in even greater contrast to the ventral pituitary surface because of its more marked convolution. The third ventricle communicates with the infundibular process

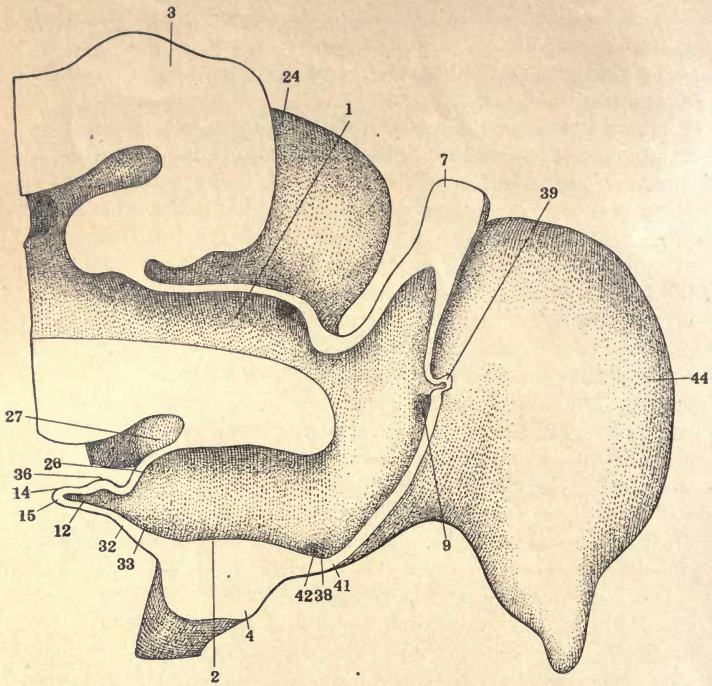

Fig. 21 Mesial view of forebrain reconstruction of 14 days and 18 hours chick. × 25. *1*, aqueduct of Sylvius; *2*, chiasmatic process; *3*, cerebellum; *4*, optic chiasm; *7*, epiphysis; *9*, foramen of Monro; *12*, infundibular canal; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *24*, mid-brain; *26*, mammillary recess; *27*, mammillary body; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *36*, post-infundibular eminence; *38*, pre-chiasmatic recess; *39*, paraphysis; *41*, supra-optic groove; *42*, supra-optic recess; *44*, telencephalon.

by an extremely small canal, while the infundibular recess presents many branching subdivisions which extend to the several diverticula of the dorsal convoluted surface. The post-infundibular eminence occupies its characteristic position and has not changed in size. It still retains the post-infundibular recess of the ventricle.

In the mammillary region the processes initiated in the stage of eight days have now proceeded to such a degree that the lateral mammillary recesses have become obliterated and the mammillary bodies are now solid, containing no recess accessory to the third ventricle. There is still a slight remnant of the median mammillary recess (*26*), but this also has been considerably reduced in size.

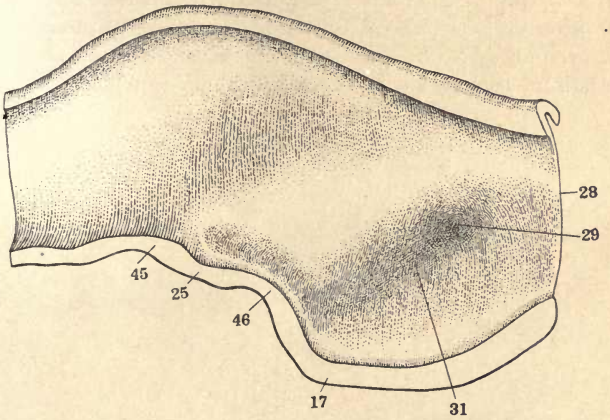

Fig. 22 Mesial view of forebrain reconstruction of 3 mm. Mustelus laevis. × 150. The unshaded area shows the cut surfaces of the reconstruction. *17*, infundibular region; *25*, mammillary region; *28*, neuropore; *29*, optic vesicle or evagination; *31*, optico-infundibular groove; *45*, tuberculum postero-superius; *46*, tubercle of the floor of Schulte.

Development of the diencephalic floor in Mustelus laevis

Mustelus embryo of 3 mm.; Specimen No. 722 (fig. 22). The embryo of this stage corresponds closely to the cat embryo of eight somites and is also similar to the chick embryo of that size. The neuropore (*28*) is still widely open, while the optic vesicle (*29*) forms the only structure at the cephalic extremity of the neural tube. Ectally this vesicle is represented by a marked lateral protuberance of the neural wall whose axis is oblique and whose apex is directed caudad. The surface relief of the brain at this stage is shown in figure 23. Dorsal to the

apex of the optic vesicle is a shallow groove which traverses the tube transversely and demarcates the vesicle from a prominent eminence, the mammillary region (*25*). The ental surface of this model (fig. 22) shows the optic vesicle as a shallow evagination from the deepest portion of which a sulcus may be traced ventrad and caudad to the tubercle of the floor (*46*). This is the optic sulcus. The ectoptic zone has not yet made its appearance. The mammillary region is well defined both as an ectal protuberance and an ental recess. The prosencephalon thus presents the two primitive constituents which are characteristic of this period in the cat and chick.

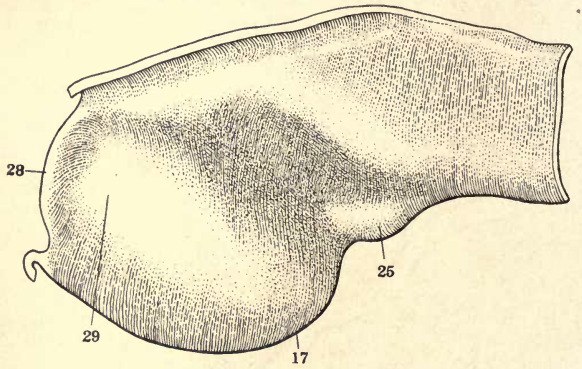

Fig. 23 Ectal view of forebrain shown in figure 22. × 150. The unshaded area shows the cut surfaces of the reconstruction. *17*, infundibular region; *25*, mammillary region; *28*, neuropore; *29*, optic evagination.

Mustelus embryo of 7 mm.; Specimen No. 294 (fig. 24). In this embryo the neuropore is still open, while the advance in development is indicated by the marked reduction of the optic vesicle (*29*) and the appearance of an ectoptic zone (*8*) presenting the three characteristic segments. The dorsal and cephalic segments present respectively the anlages of the thalamencephalon (*43*) and telencephalon (*44*), while the ventral segment now appears in the form of a definite infundibular region (*17*). The reduction of the optic vesicle has been carried to such a degree that the optic cup and optic peduncle may both be dis-

tinguished, the former manifesting as yet but slight cupping, the latter a definitely constricted stem attaching to the lateral wall of the forebrain. The prosencephalic ventricle extends through the optic peduncle into the spacious recess of the eye-cup. The vertical segment of the optic sulcus is not present,

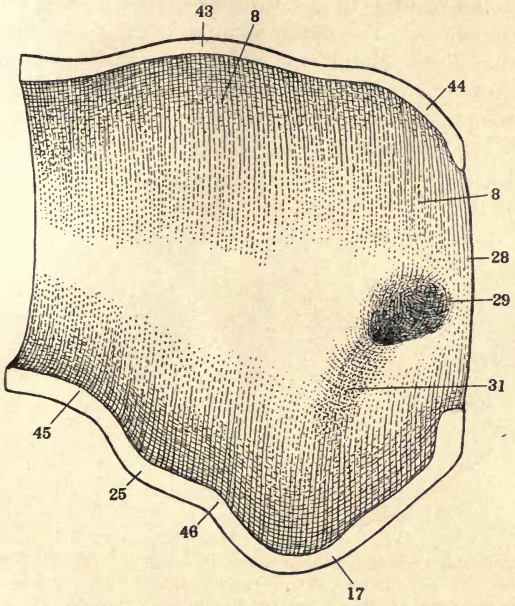

Fig. 24 Mesial view of forebrain reconstruction of 7 mm. Mustelus laevis. × 150. The unshaded area shows the cut surfaces of the reconstruction. *8*, ectoptic zone of Schulte; *17*, infundibular region; *25*, mammillary region; *28*, neuropore; *29*, optic evagination; *31*, optico-infundibular groove; *43*, thalamencephalon; *44*, telencephalon; *46*, tubercle of the floor of Schulte.

but the optico-infundibular groove (*31*) passes in the position of the horizontal segment of the sulcus from the orifice of the optic peduncle (*29*) ventro-caudally to the side of the floor tubercle (*46*). The infundibular and mammillary regions present little change in size. The tuberculum postero-superius (*45*) is not prominent.

Mustelus embryo of 11 mm.; Specimen No. 729 (fig. 25). The midbrain flexures are present in this embryo and have caused deflections of the neural axis at the anterior and at the posterior isthmian sulci. The ectoptic zone now gives more definite evidence of its ultimate derivatives, the dorsal segment showing

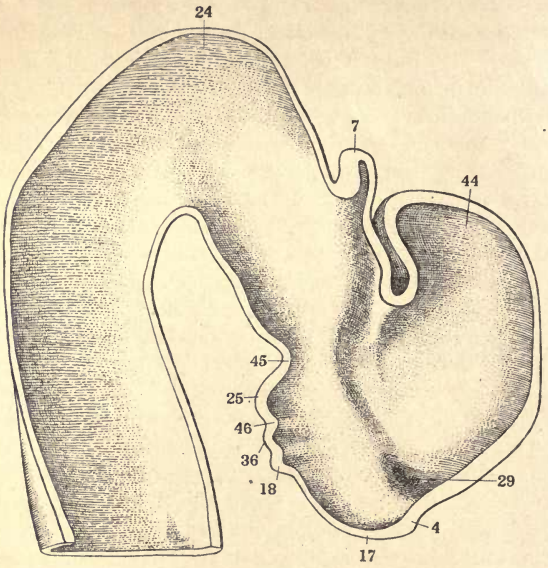

Fig. 25 Mesial view of forebrain reconstruction of 11 mm. Mustelus embryo. × 100. The unshaded area shows the cut surfaces of the reconstruction. *4*, chiasm; *7*, epiphysis; *18*, infundibular evagination; *24*, mid-brain; *25*, mammillary region; *29*, optic evagination; *36*, post-infundibular evagination; *45*, tuberculum postero-superius; *46*, tubercle of the floor of Schulte.

the characteristic thalamencephalic formation, while the cephalic segment presents all of the primitive elements of the telencephalon. The ventral segment of the ectoptic zone is considerably modified. The infundibular region (*17*) has not only increased in size, but at its apex or caudal portion two evaginations have made their appearance. Of these the infundibular evagination (*18*) is more extensive but less protuberant. The pituitary anlage is

in contact with the ectal surface of this evagination, except for a small area immediately ventrad to the dorsal evagination. In these respects the development of Mustelus corresponds in all details to that of the cat and of the chick. The post-infundibular evagination (*36*) is the smaller of these secondary protuberances. Upon its ventricular surface it is demarcated from the mammillary region by a distinct elevation, the tubercle of the floor (*46*). Ventrally it becomes continuous with the ventral infundibular evagination (*18*).

The mammillary region (*25*) has attained a sharper outline without appreciable increase in size. It is assuming the characteristics which lead to the recognition of it as the posterior lobe. The optic vesicle is relatively smaller than the forebrain; its peduncle (*30*) has become more constricted except at its proximal extremity where it presents a slight dilatation into which extends a recess accessory to the ventricle. The optic peduncle still retains its canal which communicates with the residual lumen of the optic cup. The optico-infundibular groove is less well defined than in the earlier stages.

Mustelus embryo of 20 mm.; Specimen No. 730 (figs. 26). In this embryo the anterior and posterior isthmian flexures are present and well marked. All of the elements described in the 11 mm. embryo may be recognized and are but little changed. The principal advances are seen in the thalamencephalon and telencephalon. In the infundibular region, however, a process of importance has been initiated and has already assumed considerable proportions. During the earlier stages it has been in the apex or caudal portion of this region that notable changes were observed. Now and for some time to follow the development of its cephalic portion becomes more conspicuous and salient. Following the ventral border of the optic peduncle, some optic fibers have already made their way inward to form the chiasm (*4*); the floor of the ventricle at the same time has been slightly elevated above the chiasm as a transverse ridge passing between the orifices of the optic peduncles. This ridge, the chiasmatic process (*2*), separates the prechiasmatic and postchiasmatic recesses. Of these the latter is the more prominent

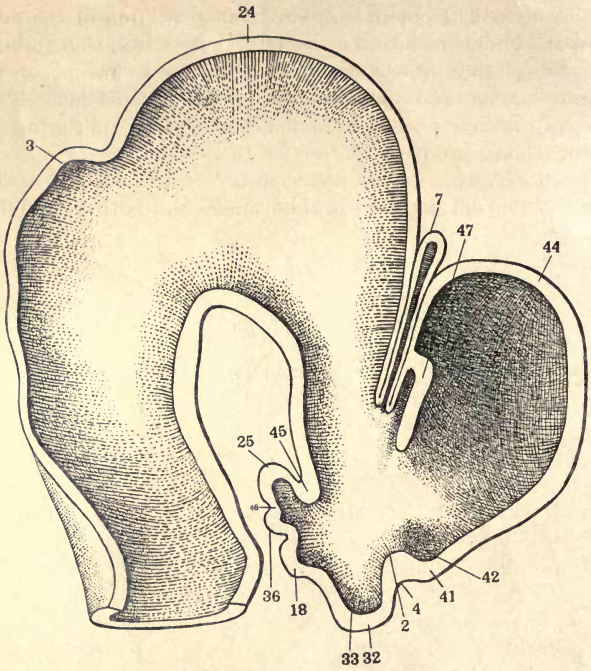

Fig. 26 Mesial view of forebrain reconstruction of 20 mm. Mustelus. × 75. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *3*, cerebellum; *4*, chiasm; *7*, epiphysis; *18*, infundibular evagination; *24*, mid-brain; *25*, mammillary region; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *36*, post-infundibular eminence; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon; *46*, tubercle of the floor of Schulte; *47*, velum transversum.

and has expression upon the surface in a large protuberance caudal to the chiasm, the post-chiasmatic eminence. This eminence already shows a demarcation into a shallow post-chiasmatic groove in which the ventricular floor is thin and two large, thick-walled protuberances, the lateral processes of the post-chiasmatic eminence or inferior lobes. The cavity of the

ventricle extends from the narrow median portion of the post-chiasmatic eminence into the two lateral processes, thus forming the recessus lobi inferioris. From the dorsal region of the pituitary anlage two sprouts, each as yet independent of the other, are growing forward along the ventral surface of the median post-chiasmatic groove.

Mustelus of 50 and 70 mm.; Specimens Nos. 725 and 735 (figs. 27 and 28). The development in these stages has carried the differ-

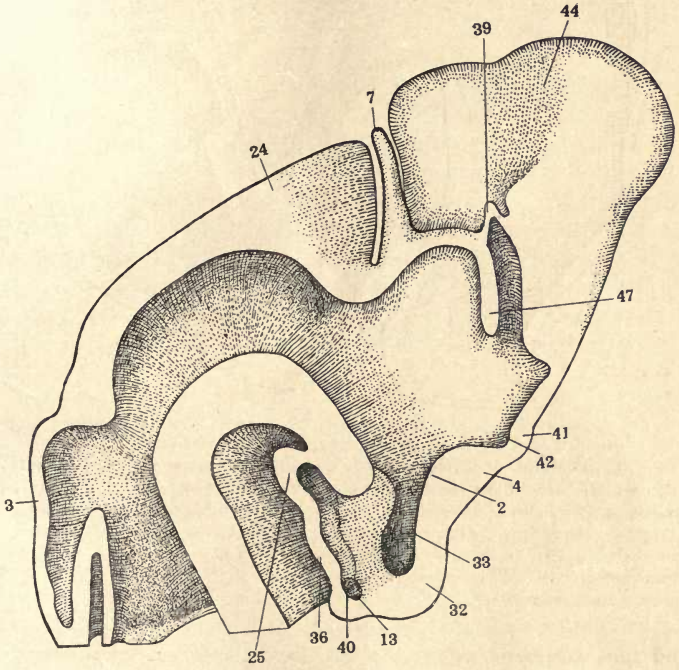

Fig. 27 Mesial view of forebrain reconstruction of 50 mm. Mustelus. × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *7*, epiphysis; *13*, infundibular process; *24*, mid-brain; *25*, mammillary region; *32*, post-chiasmatic eminence (lobus inferior); *33*, post-chiasmatic recess (recess of inferior lobe); *36*, post-infundibular evagination; *39*, paraphysis; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon; *47*, velum transversum.

entiation of the post-chiasmatic eminence still further and makes it possible to recognize more clearly in the two lateral processes of this eminence the anlages of the *lobi inferiores*. The median post-chiasmatic groove remains as a narrow strip of the brain floor in which the tissue is relatively thin, while the inferior lobes are becoming massive, thick-walled bodies. The recess

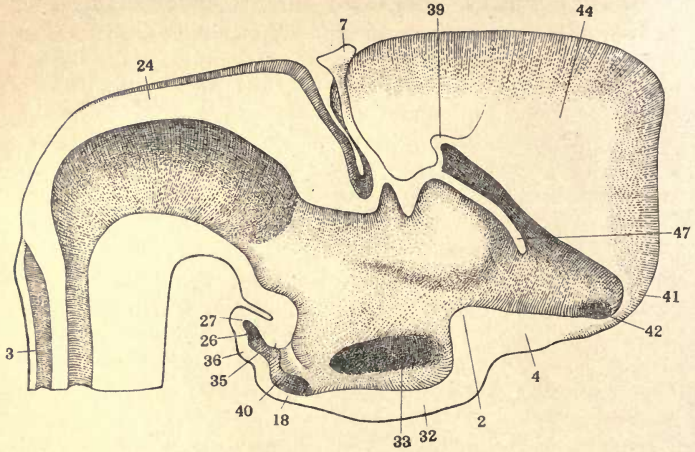

Fig. 28 Mesial view of forebrain reconstruction of 70 mm. Mustelus. × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *7*, epiphysis; *18*, infundibular evagination; *26*, mammillary recess; *27*, mammillary body (posterior lobe); *32*, post-chiasmatic eminence (inferior lobe); *33*, post-chiasmatic recess (recess of inferior lobe); *35*, post-infundibular recess; *36*, post-infundibular eminence; *39*, paraphysis; *40*, recess of infundibular process; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon.

of the ventricle in relation with the region of the median groove extends laterad upon both sides into the inferior lobes. The chiasmatic process (*2*) has increased in size and consequently projects further into the ventricle, thus accentuating the boundaries of the prechiasmatic and post-chiasmatic recesses. The former recess may be traced laterad into a small canal which overlies the optic chiasm and the proximal portion of the optic

nerve, the supraoptic recess (*42*). The caudal portion of the infundibular region presents no change of moment. The two sprouts of the pituitary anlage which extend along the ventral surface of the median post-chiasmatic groove are still independent of each other except for a small area near their point of origin where they seem to have undergone fusion across the median line. The mammillary region (*25*) has extended to some degree laterally so that now there are added to the original median evagination of this region two slightly projecting lateral processes into which the cavity of the ventricle extends. In the 70 mm. Mustelus the inferior lobes are more prominent and the pituitary sprouts extending along the ventral surface of the median post-chiasmatic groove have now united throughout their entire length, thus forming a tongue-like projection of the pituitary gland. The mammillary region in this stage has attained all of the characteristics of the posterior lobe (*27*), presenting a median portion and two lateral processes which project free. In the caudal area of the infundibular region the only notable change is in the apparent expansion of the ventral evagination in that portion immediately ventral to the dorsal evagination. This is an area which is not in contact at any point with the pituitary gland.

Mustelus of 100 and 300 mm.; Specimens Nos. 726 and 694 (figs. 29 and 30). In both of these late stages the angle in the neural axis at the posterior isthmian sulcus has disappeared. The optic chiasm (*4*) and chiasmatic process are larger, thus accentuating the prechiasmatic (*38*), and the post-chiasmatic (*33*) recesses. The supraoptic recess (*42*) extends as a small canal along the cephalic surface of the chiasm and the proximal portion of the optic nerve. In the post-chiasmatic eminence (*32*) the inferior lobes and the median post-chiasmatic groove may be definitely recognized. In the groove rests the tongue-like extension of the pituitary gland. The posterior lobe (*27*) has increased in size, especially in its lateral processes, each of which contains an accessory recess of the ventricle. More prominent changes, however, have appeared in the caudal portion of the infundibular region and particularly in the ventral

evagination (*18*). Here growth has been more pronounced than in any other of the neighboring parts. This growth has affected the area immediately ventrad to the dorsal infundibular evagination which in this stage of 70 mm. had already shown signs of expansion. The result of the growth is the formation of an infundibular process (*13*) which consists of a smooth, membranous, but as yet non-vascular, dorsal surface not in contact with

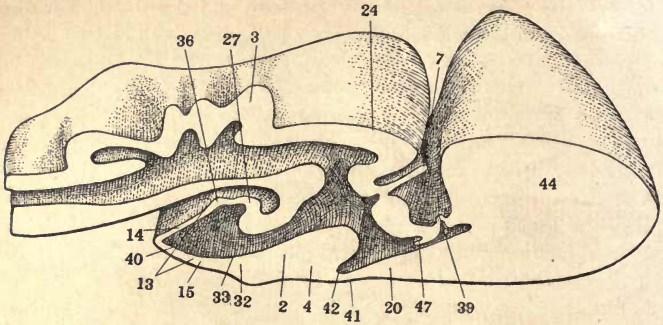

Fig. 29 Mesial view of brain reconstruction of 100 mm. Mustelus. × 25. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *3*, cerebellum; *4*, chiasm; *7*, epiphysis; *13*, infundibular process; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *24*, mid-brain; *27*, mammillary body (posterior lobe); *32*, post-chiasmatic eminence (lobus inferior); *33*, post-chiasmatic recess (recess of inferior lobe); *36*, post-infundibular evagination; *40*, recess of infundibular process; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon; *47*, velum transversum.

the pituitary gland, the saccular surface (*14*) and a thicker surface in contact with the gland, the pituitary surface (*15*). In the 100 mm. Mustelus the saccular surface presents no sign of convolution or blood vessels; in the 300 mm. Mustelus the tendency toward the production of complicated diverticula in this surface is evident, as well as a rapidly advancing vascularization. These changes mark the inception not only of the diverticula sacci vasculosi, but also of the rich blood supply which gives the saccus vasculosus its name. In addition to the diverticula sacci vasculosi there is a portion of the recess of the infundibular

process which, because of its close relation to the pituitary gland, is called the recessus hypophyseus (*10*). The pituitary and saccular surfaces of the infundibular process are continued laterad for a considerable distance forming two tapering extensions, the lateral processes of the processus infundibuli. During this development the dorsal infundibular evagination (*36*) manifests but little change; when, however, the infundibular process is formed the dorsal evagination, because of its position, becomes the post-infundibular eminence.

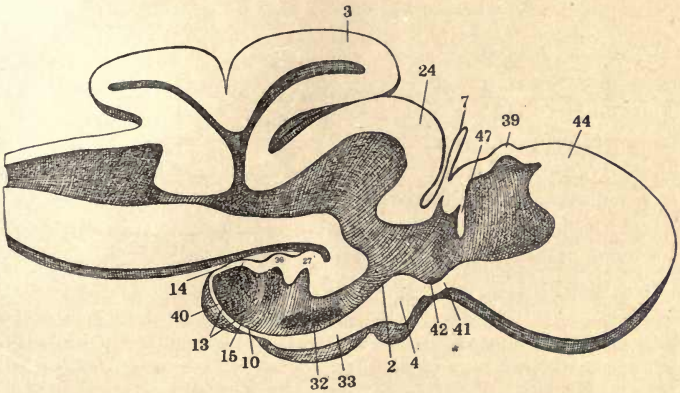

Fig. 30 Mesial view of brain reconstruction of 300 mm. Mustelus. × 25. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *3*, cerebellum; *4*, chiasm; *7*, epiphysis; *10*, hypophyseal recess; *13*, infundibular process; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *24*, mid-brain; *27*, mammillary body (posterior lobe); *32*, post-chiasmatic eminence (inferior lobe); *33*, post-chiasmatic recess (recess of inferior lobe); *36*, post-infundibular evagination; *39*, paraphysis; *40*, recess of the infundibular process; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon; *47*, velum transversum.

The ontogenesis of the diencephalic floor in Mustelus, as in the cat and chick, may thus be traced from two primitive forebrain elements, the optic vesicle and the mammillary region. From the optic vesicle is derived the ventral segment of the ectoptic zone which gives rise to the infundibular region. From the optic vesicle the following structures are derived, i.e., the retina,

optic nerve and chiasm, chiasmatic process, prechiasmatic and supraoptic recesses of the third ventricle. The derivatives of the ventral evagination of the infundibular region in Mustelus are the inferior lobes, median post-chiasmatic groove and the infundibular process (including the pituitary surface, the saccus vasculosus and the lateral processes of the saccus). From the dorsal evagination arises the post-infundibular eminence. The mammillary region becomes the posterior lobe.

DISCUSSION

A review of the literature covering the diencephalon reveals certain difficulties imposed upon this region by terminology. These difficulties are especially pronounced in the basal region of the interbrain, which His (10) has called the *hypothalamus*. The advantage of this term in the adult human brain, as well as in other mammalian forms, is obvious; but it loses its precision when applied to many of the lower vertebrates. There is much to recommend the term *hypencephalon* (Unterhirn) suggested by von Kuppfer (7). This, however, refers to a somewhat arbitrary subdivision of the diencephalon, and von Kuppfer himself is not always consistent in its application, since in some instances he uses it as the equivalent of the hypothalamus, while in others he restricts it to the basal area of the interbrain, exclusive of the infundibulum. The latter element, 'infundibulum,' more perhaps than any other part in this region, has been a source of confusion. Johnston's (11) objections to the use of the term 'infundibulum' seem well founded. As he points out, the application of this term to a relatively extensive embryological area and also to a much more restricted portion of the adult brain is almost certain to be misleading. Usage, however, has given it a permanency in the literature and in addition to this the phylogenetic significance attached to the part by some investigators cannot be overlooked. As already stated, Ayers (2) asserts that the hypophysis arose as an organ of taste and the infundibulum was its nerve. Boeke (19) has found in Muraenoids from the third day of embryonic life until the critical

period a sharply defined area in the ventral infundibular wall clearly differentiated to form not a gland as some maintain but a sense organ of unknown significance which is functional in the early larval stages. Other pelagic teleosts present a similar structure, although not as clearly marked as in the Muraenoids.

The ectoptic zone. It has seemed to the writer that some of the discrepancies above mentioned may arise from the fact that the 'infundibulum' in the embryological sense is not one of the primitive areas of the diencephalon. It is, as already shown in the domestic cat by Schulte and Tilney (12), a secondary derivative of the primitive optic vesicle; interpreted in this light its significance seems to become more clear. In the domestic cat, the chick and the dog-fish two primitive areas may be recognized in the developing forebrain. For a considerable period before the neural folds meet in the region of the prosencephalon the optic vesicles are the only elements present. They appear at the cephalic extremity of the neural folds as prominent diverticula, one upon either side. Almost immediately after the formation of the vesicles and before the neural folds have met, there appears a recess in the floor of the prosencephalon directly caudal of the apex of the optic evagination. This recess presents a corresponding ectal protuberance which forms the mammillary region. The optic vesicle and mammillary region are consequently the primitive derivatives of the cephalic extremity of the neural tube. These observations are true of the cat, chick and dog-fish. In the subsequent evolution of the prosencephalon the optic vesicles play the more important rôle of these two primitive derivatives. For a period prior to and for some time after closure of the neuropore this vesicle undergoes a profound remodelling, as a result of which the optic evaginations become reduced in size and an ectoptic zone appears in the form of an arc about the vesicle. This arc presents a dorsal, a cephalic and a ventral segment, the latter being the last to make its appearance. When, however, it has appeared it constitutes a well defined area, the infundibular region.

It has already been shown (p. 233) that the telencephalon arises from the cephalic segment of the ectoptic zone, while the

thalamencephalon takes origin in the dorsal segment. From these facts it seems fair to assume that the third element of this zone, namely the ventral segment, possesses similar possibilities of development and the three segments of the ectoptic zone may therefore be regarded as dynamically coördinate. The attempt to substantiate this assumption is given in discussing the derivatives of the infundibular region.

The optic vesicles. In the period of development shortly after the closure of the neuropore the floor of the forebrain consists of the lamina terminalis, the optic evaginations and the infundibular and mammillary regions. In sauropsid and mammalian forms the lamina terminalis assumes a vertical position in the later stages of development; in the ichthyopsid, on the contrary, it remains horizontal and is thus an element in the floor of the ventricle cephalad to the optic chiasm. Entally the evaginations of the primitive optic vesicles are indicated by the optic sulcus which does not in any way correspond to the preoptic and post-optic grooves of authors. This sulcus is bilateral. It does not cross the median line as the above mentioned grooves are shown to do, and in its early appearance it presents itself as an arcuate fissure consisting of a vertical and horizontal segment, the latter extending caudad to the tubercle of the floor, while the convexity of the entire arc is directed cephalad. Subsequently, when the primitive optic vesicle has become reduced by the remodelling which results in the formation of the ectoptic zone, the vertical segment of the optic sulcus disappears but the position of its horizontal segment is occupied by the optico-infundibular groove. At this stage the optic vesicle has so changed its external conformation as to have the appearance of a pedunculated diverticulum of the forebrain to which latter it is attached by a constricted, hollow stalk, the optic peduncle. In relatively late stages after the appearance of the chiasmatic process a transverse groove connects the orifices of the optic peduncles. A groove is also formed caudad to the chiasmatic process. These undoubtedly correspond to the post-optic and preoptic grooves already mentioned, but it will be noticed that their appearance developmentally is relatively late. The proximal portion of the optic

peduncle ultimately becomes expanded and contains a large recess accessory to the third ventricle which overlies the optic chiasm and proximal portion of the optic nerve. The remainder of the optic diverticulum rapidly assumes the characteristic form of the eye-cup, while the cavity between its ental and ectal layers communicates with the third ventricle by means of the optic peduncle, retaining this communication until a late period of embryonic life. Ultimately the lumen of the distal portion of the peduncle becomes obliterated. In the adults of all the forms examined a marked prechiasmatic recess of the ventricle is present. It is continued laterad along the dorso-cephalic margin of the chiasm and for some distance above the optic nerve as the supraoptic recess. The position of these recesses is indicated upon the surface by a ridge which traverses the chiasm and proximal portion of the nerve, the supraoptic crest. This likewise is constant in all the forms examined. Osborn (13), Herrick (14) and Kingsbury (15) have shown that the rudimentary condition of the eye in Necturus is accompanied by a similar condition of the optic nerve which retains the primitive lumen of the optic vesicle and is hollow for a considerable distance peripherad. This fact and the embryological evidence make clear the homologies of the supraoptic crest, chiasmatic process, prechiasmatic and supraoptic recesses in the adult.

The infundibular region. The infundibular region presents greater difficulties for analysis. These doubtless are due to the fact that the ventral segment of the ectoptic zone, like the cephalic and dorsal segments, is capable of marked adaptive variations. As seen in the elasmobranch, for example, the main feature of this region is the so-called *hypoarium* described and first so named by Sanders (16). The hypoarium consists of two large symmetrical eminences situated one on either side of the mid-sagittal line immediately caudad to the optic chiasm and containing an extension of the third ventricle. In their general conformation they are not unlike the optic lobes of the midbrain; they are usually termed the *lobi inferiores.* In many teleosts these lobes are still further subdivided forming on either side a large lateral lobe and a small inferior lobe, both of which

contain extensions of the third ventricle. In amphibia the inferior lobes are prominent elements derived from the infundibular region, while in sauropsids and mammals the tendency to the formation of the extensive hypoarium appears to have ceased and no corresponding structures are to be found in the position of the inferior lobes. Fritsch (17) suggested the homology of these structures with the corpora mammillaria, but Herrick (14) and others have shown conclusively that this suggestion is not well founded. The significance of the inferior lobes becomes more apparent in the light of their embryological history. As already stated, the infundibular region in embryos of the dogfish, chick and cat is a secondary derivative from the primitive optic vesicles. After this region has made its appearance the portion immediately caudad to the optic chiasm undergoes certain changes which in the selachian terminate in the formation of the inferior lobes. The development of these structures as definitive elements in the floor of the diencephalon begins at a relatively late period and is characterized by the growth of a diverticulum immediately behind the chiasm in such a way that two symmetrical evaginations are formed, each containing an extension of the third ventricle. These bilateral evaginations at first have thin walls but they grow rapidly, the walls becoming thicker and the cavity contained within them being correspondingly reduced in size. In the bird the same tendency to the formation of a large diverticulum immediately caudad to the chiasm is observed. This diverticulum in the relatively late stages tends to become divided into two symmetrical evaginations and at this stage resembles in all details the early formation of the inferior lobes in the selachian. Thereafter, however, the impetus toward the formation of the typical ichthyopsid hypoarium appears to cease. The evaginations remain comparatively thin-walled and finally become a fairly prominent post-chiasmatic eminence. A similar course of events is observed in the mammal as illustrated by the development of the domestic cat. Here the infundibular region caudad to the chiasm at first forms a diverticulum which later becomes subdivided sagittally in such a way as to present two bilateral evaginations. The conditions

observed in this region in the cat embryo of 25 mm. length almost exactly duplicate those in the brain of the 20 mm. Mustelus, but as in the case of the chick, the tendency of this region to give rise to large inferior lobes diminishes as growth progresses and in the fetal stages the only evidence of this tendency is to be found in the large post-chiasmatic eminence and the post-chiasmatic recess. Significant in this connection also is the relation which the pituitary gland bears to this part of the infundibular region. As the writer (8) has already shown, the post-chiasmatic eminence in the cat and chick comes to be invested by a secondary outgrowth from Rathke's pocket which ultimately forms the pars tuberalis of the gland. In the selachian no such investment of the inferior lobes takes place, but the tuberal portion of the gland by a process of development similar to that in the bird and mammal grows forward and occupies a juxta-neural position in contact with the small portion of the infundibular region which forms the median post-chiasmatic groove.

The caudal portion of the infundibular region including the apex is involved in the formation of the neural portion of the hypophysis. In its inception the developmental process of this part in all the forms studied presents a marked similarity. The area about the apex of the infundibular region undergoes a subdivision so that two evaginations are formed, one dorsal and the other ventral. In the cat this subdivision gives the dorsal evagination the greater size from its beginning, while in the bird and the dog-fish the ventral evagination is the larger. In all instances the ventral evagination proceeds to the formation of the neural portion of the hypophysis, the infundibular process. In the salachian this process is but little pedunculated. A slight constriction does, however, occur and justifies the term infundibular process for the structure which is connected with the floor of the interbrain by a short infundibular stem. The characteristic features of this infundibular process are the development of two morphologically different surfaces one which is ventral, thin and non-convoluted coming in contact with the pituitary gland, the other which is thin-walled and dorsal in position, but

having no contact with this gland. The ventral surface because of its relations may be called the pituitary surface, the dorsal one because of its participation in the formation of the saccus vasculosus, the saccular surface. These two surfaces are present in the bird; but in the cat, although the dorsal surface of the infundibular process is much thinner than its ventral surface, there is no other evidence of the tendency toward saccus formation. As development proceeds in the selachian, the pituitary surface maintains its primitive relations unchanged while the saccular surface becomes more extensive and in Mustelus at the period of 20 cm. shows the first evidence of a rich vascularization and the tendency of its thin wall to be thrown into numerous convolutions typical of the saccus vasculosus. The pituitary and saccular surfaces extend laterad for a considerable distance, their size being reduced as they extend farther away from the median line so that they ultimately form two long tapering outgrowths, one at either extremity of the infundibular process, called the lateral processes. Similar outgrowths are observed in the development of the bird, and while no definitely corresponding structure is found in the cat, the lateral extremities of the infundibular process are much extended in a manner which seems to be reminiscent of the lateral processes in the bird and selachian. In the bird, as already shown, the dorsal surface of the infundibular process is convoluted but non-vascular; its walls are thick. All of the morphological evidence concerning it tends to show that this surface is the strict homologue of the saccular surface in the selachian, and that, whereas in the fish it proceeds to form the saccus vasculosus, the saccus formation in the bird is aborted, although the sauropsid still retains evidence of the tendency toward the formation of this structure. Furthermore, the late stages of embryonic life in the bird correspond in many details to the saccus formation as it appears in this region of the selachian.

In the mammal, as illustrated by the cat and other Felidae, there is nothing which suggests the saccus formation in any part of the infundibular process further than the very thin dorsal surface which is emphasized, in the early stages, by the rapid

growth and thickness in the ventral wall of the infundibular process. This, together with the fact that in the Felidae an extension of the third ventricle is contained in the infundibular process, points strongly to the conclusion that the dorsal wall of this process in embryonic stages may be homologized with the saccular surface just described in the other forms. That this area in mammals becomes invested by the pars infundibularis of the pituitary gland, may be interpreted as causing the retrogression of the saccular surface and its replacement by a new area in contact with tissue of the pituitary gland, due to the greater extension of the infundibular portion of this gland in mammals.

Discussing the significance of the saccus vasculosus and its more characteristic formation in the water-living types of reptiles, Edinger (18) suggests that it may be an apparatus of especial importance to aquatic animals. This inference, however interesting, is not borne out by the facts observed in some of the aquatic mammals, since there is no evidence of anything corresponding to the saccus vasculosus or even an abortive saccus-formation in Castor canadensis or in Macrorhinus angustirostris. The absence, therefore, of any attempt to revert to the formation of a saccus vasculosus in mammals, even though they be water-living, fails to corroborate Edinger's suggestion that this apparatus is an adaptation peculiar to aquatic life. It seems more probable that the disappearance of the saccus vasculosus depends upon a profound remodelling of the forebrain which occurs in passing from ichthyopsid to the sauropsid and mammalian forms. It is not unlikely that this highly vascularized structure is closely related to if not identical with the chorioid formations and represents in the fish a means of supplying an extensive chorioidal plexus to the third ventricle, particularly as such plexuses are relatively small in other parts of the diencephalon.

The dorsal evagination of the infundibular region still remains to be considered. As already stated, this evagination in the cat is of greater size than the ventral one from which latter the infundibular process is derived. In the bird and the dog-fish

the reverse is true. The evagination is present in the early stages in the selachian and may be traced through to adult life, when it occupies a position immediately ventral of the posterior lobe and dorsal to the saccus vasculosus. Similarly in the bird it lies dorsal to the infundibular process from its inception and maintains this position in the adult. Its development in the cat is equally clear; here it forms a protuberance of the diencephalic floor caudal to the infundibular stem and in front of the mammillary bodies; this has been called by the writer the post-infundibular eminence. Much discussion has arisen concerning this element of the interbrain. Retzius (9), who first described it in mammals, considered that it was the homologue of the saccus vasculosus in fishes. Staderini (20), however, states that topographically, as well as from its developmental relations, the saccus vasculosus can bear no relation to the *eminentia saccularis*. It is also his opinion that nothing in the intimate constitution of the saccular eminence favors the conception of Retzius. In fishes the saccus vasculosus is a thin-walled structure connected with a great number of blood vessels. In man and other mammals the structure referred to by Retzius is a relatively thick-walled evagination with scanty vascularization. Sterzi (21) is unwilling to accept the interpretation of Retzius given to the eminentia saccularis, and believes that the saccus vasculosus has nothing in common with the latter either in position or structure, while Perna (22) on histological grounds maintains that there can be no homology between the saccus vasculosus and the so-called 'saccular eminence.'

The post-infundibular eminence has been shown in illustration by many authors in a number of different species, although it has not always been definitely referred to in their text. Herrick and Obenchain (23) in their reconstruction of the brain of Ichthyomyzon concolor figure a small, unleadered eminence ventrad to the mammillary body, in which there appears on mid-sagittal section a small recess communicating with the third ventricle. The only reference to this element made by these authors is the attention which they call to the fact that the *post-infundibular commissure* passes through the more cephalic portion of the structure.

In surface relief, however, it forms a prominent element in their illustration of the diencephalic floor in this form. Sterzi (21) in his illustrations of Acanthias vulgaris (80 cm. long), in Mustelus laevis (30 cm. long) and in Raja clavata (60 cm. long) shows a similar structure dorsal to the saccus vasculosus and ventral to the posterior lobe although in none of these cases has he included this element in his description. Burckhardt (24) shows a similar condition in Protopterus annectans. In the ontogenesis of the dog-fish, of the chick and of the cat the dorsal evagination of the infundibular region is a constant element and may be traced through successive stages until the definitive post-infundibular eminence has made its appearance. Thus the embryological history of the infundibular region seems to make clear the fact that the inferior lobes may be homologized with the post-chiasmatic eminence. The infundibular process, including as it does the saccus vasculosus of the ichthyopsid, is the homologue of the infundibular process in the sauropsid and mammal, although in these latter forms the saccus formation is retrogressive or absent. In this respect the writer agrees with Johnston (11) and concurring with him can find no evidence to support Edinger's (18) idea as embodied in his schematic figure of a sagittal section of the vertebrate brain which shows an infundibular process in contact with the pituitary gland while dorsal to it is an entirely separate evagination of the brain floor which he calls the saccus vasculosus. It seems equally clear that the homology of the post-infundibular eminence may be established throughout the phylum. That it is an element separate and distinct from the saccus vasculosus is evident from the ontogeny of the selachian in which both a saccus vasculosus and a post-infundibular eminence are present. There can be no grounds, therefore, for the homology suggested by Retzius (9) between the 'saccular eminence' of mammals and the saccus vasculosus of fishes.

Although the fact has not been fully established, the evidence furnished by the ontogenesis of the dog-fish, of the chick and of the cat strongly suggests that the derivatives of the three segments of the ectoptic zone are coördinate. In this light the

telencephalon derived from the cephalic segment, the thalamencephalon from the dorsal segment and the infundibular region from the ventral segment are developmental equivalents. It has been shown that from the infundibular region in the ichthyopsid the inferior lobes, the infundibular process and the post-infundibular eminence are derived. If, as has been assumed to be the case in fishes, the inferior lobes are chiefly concerned in the gustatory sense, the telencephalon in the olfactory sense and the thalamencephalon in the somaesthetic senses, then there is further reason to believe that the derivatives of the three segments of the ectoptic zone are functionally of the same order. The disappearance of the inferior lobes in passing from the ichthyopsid to the sauropsid is, as a process, no more difficult to comprehend than the similar disappearance of the optic lobes of the midbrain in the transition from the bird to the mammal. In each instance this process seems to be accomplished by the addition of neopallial areas which assume the functions of the more primitive brain parts. The significance of the persistence of the infundibular process and the post-infundibular eminence is less clear, although in the former case this doubtless is involved in the adaptive variations of the pituitary gland, while in the latter the post-infundibular commissure may be a determinative factor.

The tuber cinereum is usually described as an area in the basal region of the diencephalon, bounded cephalad by the optic chiasm, caudad by the mammillary bodies and laterad by the optic tracts and cerebral peduncles. This area in mammals includes the post-chiasmatic eminence, the lateral eminences and the post-infundibular eminence. From the embryological standpoint, the tuber cinereum comprises all of the derivatives of the infundibular region except the infundibular process and its stem. To hold the tuber to this interpretation in fishes and amphibia would necessitate the inclusion in it of the inferior lobes, but since this has no apparent advantage in the lower forms mentioned it is, perhaps, well to confine the term *tuber cinereum* to mammals, in which instances it is useful in referring to a distinctive region of the diencephalic floor. The homology of the

lateral eminences of the tuber is not clear in the light of the material studied. Conditions in the teleost, however, in which the hypoarium presents small lobi inferiores and much larger lobi laterales, may be regarded as suggestive, since the progressive reduction of the inferior lobes has been shown to result in the formation of the post-chiasmatic eminence and a similar diminution of the lateral lobes might, therefore, determine the eminentiae laterales hypencephali. This homology is tentatively offered, since it requires further proof in the development of the teleost to establish it.

The mammillary region. The posterior lobe is the most caudal structure in the diencephalic floor of the selachian. Its relations have already been described (page 231). It consists of a median portion and two lateral processes which project free, one upon either side. Its characteristic feature appears in the fact that it contains a large recess of the third ventricle which extends from the median portion into the two lateral processes. Sterzi (21) has figured and described the posterior lobe in selachians; von Kuppfer (7) has shown it in Bellostoma, Squalus acanthius, and Necturus. Edinger (18) describes it in the selachian as the lobus posterior sive saccus infundibuli. Johnston (11) shows the posterior lobe as well as the post-infundibular eminence in a figure of the mesial surface of the right half of the brain in Squalus acanthius, although neither of these structures is specifically named by him in this place. Herrick and Obenchain (23), in their illustration taken from the reconstruction of the brain in Ichthyomyzon concolor, indicate a structure similar in relations and characteristics to the posterior lobe which they call the corpus mammillare. In several respects the designation given the structure by the last named authors seems to be most in keeping with the facts, for although the majority of investigators have employed the term *posterior lobe* in selachian and teleosts, the embryological history of the structure clearly shows that it is derived from the primitive mammillary region. In the ichthyopsid the mammillary region develops in such a way as to form a posterior lobe presenting the characteristics already described and retaining a recess accessory to the third ventricle,

the recessus lobi posterioris. In birds and reptiles the developmental history of the mammillary region through the early stages is similar to that in the fish. Later, however, the walls of this region begin to thicken rapidly and the mammillary recess becomes progressively reduced in size until it is obliterated and the solid mammillary bodies have been formed. The marked cephalic flexure in the fowl causes a divergence in the long axes of the mammillary bodies caudo-cephalad, so that these structures do not present the same prominence here as they do in the diencephalic floor of mammals. The development of the mammillary region in the cat manifests certain peculiarities which I was unable to observe in either the chick or the dog-fish. These peculiarities appear in the formation of two relatively early diverticula, the median mammillary evagination and the dorsal mammillary evagination. The latter evagination is unquestionably involved in the formation of the *corpus interpedunculare*, for I have found that the fasciculus retroflexus of Meynert may be seen passing from the *habenular region* directly to the evagination in question as early as the stage of 25 mm. There can be no doubt that this dorsal evagination, therefore, is the anlage of the corpus interpedunculare. That no similar evagination has been found either in the dog-fish or in the chick may argue that a less definite portion of the mammillary region gives rise to the corpus interpedunculare in these forms, but it is probable that this ganglionic body takes origin from the primitive mammillary region, even though no distinct evagination of its own is formed. To establish this supposition, however, it will be necessary to study the development of this region further, particularly with a view to the ontogenesis of the fiber tracts connecting the several centers involved. In the light of these facts, with the exception of this interpeduncular element, it seems warranted to homologize the ichthyopsid posterior lobe with the mammillary bodies of sauropsids and mammals.

CONCLUSIONS

The supraoptic crest, chiasmatic process, prechiasmatic and supraoptic recesses in the mammal have their definite homologues in the sauropsid and ichthyopsid.

Of the structures derived from the ventral segment of the ectoptic zone the post-chiasmatic eminence of the mammal and bird may be homologized with the inferior lobes or hypoarium of fishes, while there is some evidence which seems to indicate that the eminentiae laterales hypencephali are the homologues of the lateral lobes of teleosts.

The derivatives of the caudal portion of the infundibular region, including its apex, are the infundibular process and post-infundibular eminence.

The infundibular process in the selachian presents a pituitary and a saccular surface, the latter forming the saccus vasculosus. In the bird these two surfaces are present; the saccular surface, although it has some of the characteristics of a saccus-formation, does not present an actual saccus vasculosus. So far as may now be stated for the condition in mammals, the Felidae present an extensive pituitary surface in their infundibular process. The saccular surface, however, has lost all characteristics of saccus-formation and is in fact invested by tissue of the pituitary gland. In other mammals it is difficult to draw distinction between the pituitary and saccular surfaces of the infundibular process, and this differentiation in Mammalia would indeed be impossible were it not for the intermediate position of the Felidae in this respect between the bird, on the one hand, and the majority of mammals on the other. The lateral extensions of the infundibular process, the infundibular recess, infundibular stem and infundibular canal of the domestic cat all have their homologues in the bird and selachian. The disappearance of the saccus vasculosus from the mammal may be traced through several stages of retrogression from the dog-fish to the cat, so that the homology of the infundibular process as a whole in the mammal with that of the selachian seems to be warrantable.

The post-infundibular eminence of the mammal seems to bear a clear homology to that of the bird and selachian. The embryological evidence concerning the development of this region is strongly suggestive if not conclusive in establishing this homology. The same facts make it impossible to consider the post-infundibular eminence as phylogenetically related to the saccus vasculosus, and hence raise serious objection to the term 'eminentia saccularis' as applied to it.

There can be little doubt that the posterior lobe of the selachian is the homologue of the mammillary body in the bird and mammal.

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